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COVER: A juvenile Great Horned Owl (*Bubo virginianus*) with remnants of a recent meal and mosquitos on its eyes. The juvenile fledged from one of the northernmost recorded Great Horned Owl nests, in a witch's broom along the Middle Fork Koyukuk Valley, Alaska, USA, June 2017. See the article by Reynolds *et al.* (337–345) that investigated the diet and reproductive success of the owl at its northern range limit using both nest cameras and collection of prey remains. Photo: M. Reynolds.

Note

Another mention of Meadow Vole (*Microtus pennsylvanicus*) found in pellets of Snowy Owl (*Bubo scandiacus*) in northern Ungava Peninsula, Canada

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Abstract
The examination of raptor pellets can be used to evaluate Arctic biodiversity. We found the remains of Meadow Vole (*Microtus pennsylvanicus*) and Ungava Collared Lemming (*Dicrostonyx hudsonius*) in pellets from Snowy Owl (*Bubo scandiacus*) nesting in the northern part of the Ungava Peninsula. We differentiated the two species by visual identification and geometric morphometric analysis of molar shape. The results of our study combined with historical data suggest that most commonly used range maps of Meadow Vole should be revised.

Key words: Ungava Peninsula; Meadow Vole; *Microtus pennsylvanicus*; Ungava Collared Lemming; *Dicrostonyx hudsonius*; morphological identification

L'étude des pelotes de rejection de rapaces est utile pour évaluer la biodiversité arctique. Des restes de Campagnol de Prairie (*Microtus pennsylvanicus*) et de Lemming à Collier d'Ungava (*Dicrostonyx hudsonius*) dans des pelotes de rejections de Harfang (*Bubo scandiacus*) nichant à l'extrême nord de la péninsule d'Ungava. Les deux espèces sont séparées par identification visuelle et par l'analyse morphométrique des molaires. Les résultats de cette étude combinés aux données historiques suggèrent que les cartes de distribution les plus communément utilisées pour le Campagnol de Prairie devraient être révisées.

Mots clefs: Péninsule d'Ungava; *Microtus pennsylvanicus*; *Dicrostonyx hudsonius*; identification morphologique

The northern part of the Ungava Peninsula, Canada, is remarkable for its low rodent diversity, with some distribution maps (Hall 1981; Tamarin *et al.* 1985; Shenbrot and Krasnov 2005; Wilson *et al.* 2017) indicating the presence of only the endemic Ungava Collared Lemming (*Dicrostonyx hudsonius*). This low diversity is peculiar at this latitude, where additional rodent species are generally documented (e.g., North America: Hall [1981] and Feldhamer *et al.* [2003]; Eurasia: Ognev [1948]). However, a few records of another small rodent, Meadow Vole (*Microtus pennsylvanicus*), from the northern end of the Ungava Peninsula have not been included in general range maps by some (e.g., Hall 1981; Feldhamer *et al.* 2003; Shenbrot and Krasnov 2005; Cassola 2016; Wilson *et al.* 2017). Three records are in

the Canadian Museum of Nature (CMN): two juvenile males stored in alcohol collected before 1934 from Salliut (formerly Sugluk) on the southwest side of Hudson Strait (CMNMA 12572 and 12573), and a male study skin (CMNMA 31130) collected from the same area in 1954. Banfield's (1974: 212) range map for the species covers the entire peninsula and the 1954 record is mentioned in Desrosier *et al.* (2002) and compiled in the CMN database, as well as in the Global Biodiversity Information Facility database (Khidas and Torgersen 2021). Additional specimens were collected in 2013 by Robillard *et al.* (2013, 2017) from Deception Bay, 60 km east of Salliut Inlet. More recently, five additional specimens of Meadow Vole were snap-trapped by Fortin and Caron (2015) along with five Northern Bog Lemming (*Synaptomys*

borealis) in the northern portion of the Ungava Peninsula near the Raglan Mine. Despite these previous records, the northern part of the Ungava Peninsula has not generally been included in widely used distribution maps of Meadow Vole (e.g., Hall 1981; Feldhamer *et al*. 2003; Shenbrot and Krasnov 2005; Cassola 2016; Wilson *et al.* 2017; but see Banfield 1974).

We visually examined the teeth of small mammals collected from regurgitated pellets from Snowy Owl (*Bubo scandiacus*) nests near Salluit, northern Quebec, Canada (Figure 1), in July 2013 (see Robillard *et al.* 2013, 2017 for details) and used geometric morphometrics to differentiate and distinguish rodent species. Unlike traditional morphometrics, landmark-based geometric morphometric analyses use generalized procrustes analysis (GPA), which removes the effects of size, position, and orientation. Thus, only shape parameters remain, with a minimum loss of information (Adams *et al*. 2004).

The regurgitated pellets of undigested material from birds of prey are commonly used to assess the diversity of small to medium sized animals around the world (e.g., Chaline *et al.* 1974; Ba *et al.* 2000; Meek *et al.* 2012; McDonald *et al.* 2014; Heisler *et al.* 2016; Linchamps *et al.* 2021). Cranial and dental remains in pellets can be confidently identified to the species level, hence determining prey diversity in the environment of a predator (Chaline *et al.* 1974; Andrews 1990). The circumpolar Snowy Owl is a key predator in the Arctic tundra ecosystem. Its summer diet includes a diversity of small to medium sized animals, such as birds and hares, but generally consists mainly of rodents (e.g., Watson 1957; Gilg *et al.* 2006; Therrien *et al.* 2014; Robillard *et al.* 2017; Royer *et al.* 2019).

In July 2013, 12 Snowy Owls were captured near Salluit, Ungava Peninsula (Figure 1) and equipped with global positioning system tracking transmitters (Robillard *et al.* 2013). The transmitters were pro-
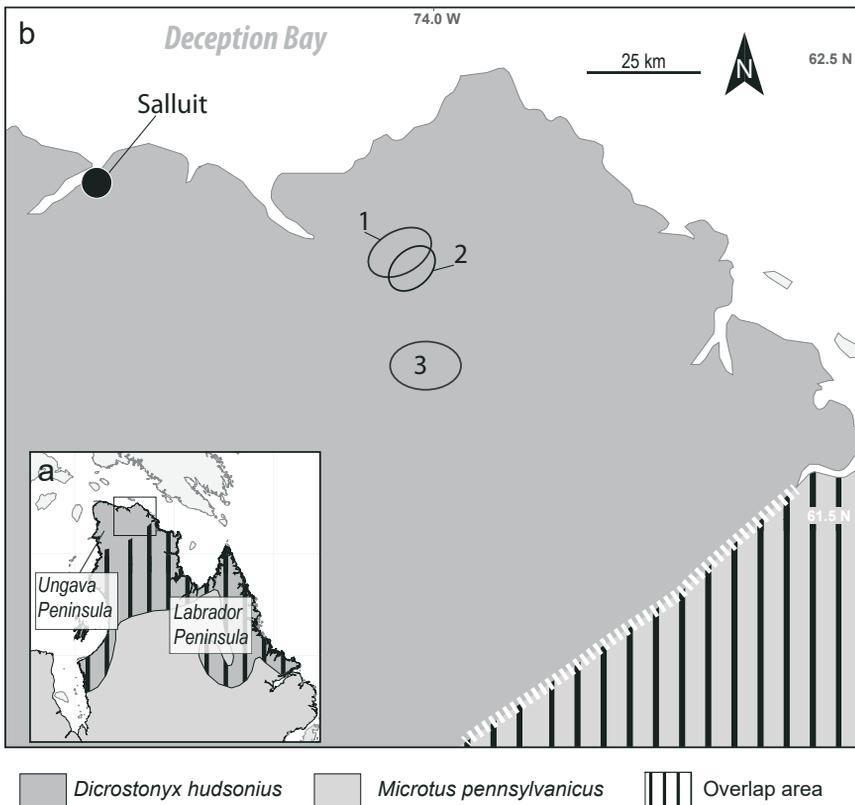
FIGURE 1. Distribution of Ungava Collared Lemming (*Dicrostonyx hudsonius*) and Meadow Vole (*Microtus pennsylvanicus*) according to Hall (1981). The black square (in a) indicates the Ragalan Mine sector from which all pellets were obtained. Specific movement ranges of the three Snowy Owl (*Bubo scandiacus*) that captured Meadow Voles are shown as ovals in b. The areas where Robillard *et al.* (2017) collected blood samples are within the owl home ranges. The dotted line indicates the erroneous northern limit of Meadow Vole (Hall 1981). Map created using the "rnaturalearth" package v.0.2.0 in R (R Core Team 2020).

grammed to communicate position every 4.5 days. Summer tracking showed that owls' movements were limited to their nesting areas. Regurgitated pellets—10 sets from 10 different nests—were collected from Snowy Owl nests a few days after the owls were captured and released (Table 1). Each pellet was dried and analysed to assess prey items from undigested materials (bones and teeth) at the Biogéosciences laboratory in Dijon, France.

Based on current distribution maps (e.g., Hall 1981; Feldhamer *et al.* 2003; Shenbrot and Krasnov 2005; Wilson *et al.* 2017; but see Banfield 1974), five rodent species can be expected throughout the entire Ungava Peninsula: Ungava Collared Lemming, Meadow Vole, Southern Red-backed Vole (*Myodes gapperi*), Northern Bog Lemming, and Eastern Heather Vole (*Phenacomys ungava*), with Ungava Collared Lemming the only species in the northern part of the peninsula. Rock Vole (*Microtus chrotorrhinus*) is mentioned at the very southern limits of the Ungava Peninsula by Desrosiers *et al.* (2002).

We identified rodent species from the owl pellets based on the morphology of the lower and upper molars following Guilday (1982), Semken and Wallace (2002), Lupien (2002), and Fauteux *et al.* (2014). Ungava Collared Lemming molars lack cementum in the re-entrant angles, unlike the four other genera (see Meadow Vole and Ungava Collared Lemming in Figure 2). The first lower molar has seven

triangles on the occlusal surface, in contrast with *Microtus* spp. with five or six closed triangles (Figure 2), *P. ungava* with five closed asymmetrical triangles, *M. gapperi* with four closed triangles on the occlusal surface, and *Synaptomys* spp. with only two closed triangles on the internal side. The most reliable criterion for separating the two *Microtus* species is the presence of an additional small "button-shaped" element at the posterior part of the second upper molar for Meadow Vole, which is always absent in *M. chrotorrhinus* (Tamarin 1985; Semken and Wallace 2002). The occlusal pattern of the third upper molar can also be a distinguishing feature, as *M. chrotorrhinus* always has a complex posterior loop, which is rare in Meadow Vole (Guilday 1982; Semken and Wallace 2002). One last criterion is the number of closed triangles on the lower second molar: *M. chrotorrhinus* has two while Meadow Vole has four.

To support this descriptive, visual identification, geometric morphometric analysis was used on the first lower molars following the protocol of Navarro *et al.* (2018) and Montuire *et al.* (2019). All teeth were first photographed using a macro objective lens (MP-E 65 mm f/2.8 on a Canon EOS6D mark II camera, Canon, Inc., Tokyo, Japan) and saved in jpg format at a resolution of 72 dots per inch. Outlines were then extracted from pictures using ImageJ v.1.52a (free software with a Public Domain License available on GitHub; Schneider *et al.* 2012). Two-dimensional

Table 1. Counts of Ungava Collared Lemming (*Dicrostonyx hudsonius*) and Meadow Vole (*Microtus pennsylvanicus*) remains found in 10 sets of Snowy Owl (*Bubo scandiacus*) pellets from Ungava Peninsula, Quebec, Canada.

Owl no.	Collection date	Rodent species	MNI*	No. left mandibles	No. right mandibles	No. skulls
2	8 July 2013	*Dicrostonyx hudsonius*	3	3	2	3
3	9 July 2013	*D. hudsonius*	17	14	17	6
		Microtus pennsylvanicus	4	4	0	2
4	4 July 2013	*D. hudsonius*	12	12	12	9
		M. pennsylvanicus	2	2	1	0
5	8 July 2013	*D. hudsonius*	1	1	1	0
6	14 July 2013	*D. hudsonius*	14	10	14	5
8	13 July 2013	*D. hudsonius*	8	8	7	6
		M. pennsylvanicus	2	1	2	1
9	—	*D. hudsonius*	5	5	4	2
		M. pennsylvanicus	2	1	2	2
10	13 July 2013	*D. hudsonius*	2	2	2	2
11	July 2013	*D. hudsonius*	3	3	1	2
Total			75			
Dicrostonyx			65 (86.7%)			
Microtus			10 (13.3%)			

*MNI = minimum no. individuals contained in the pellet, calculated for each pellet based on counts of the maxillary and left or right mandible for each species.
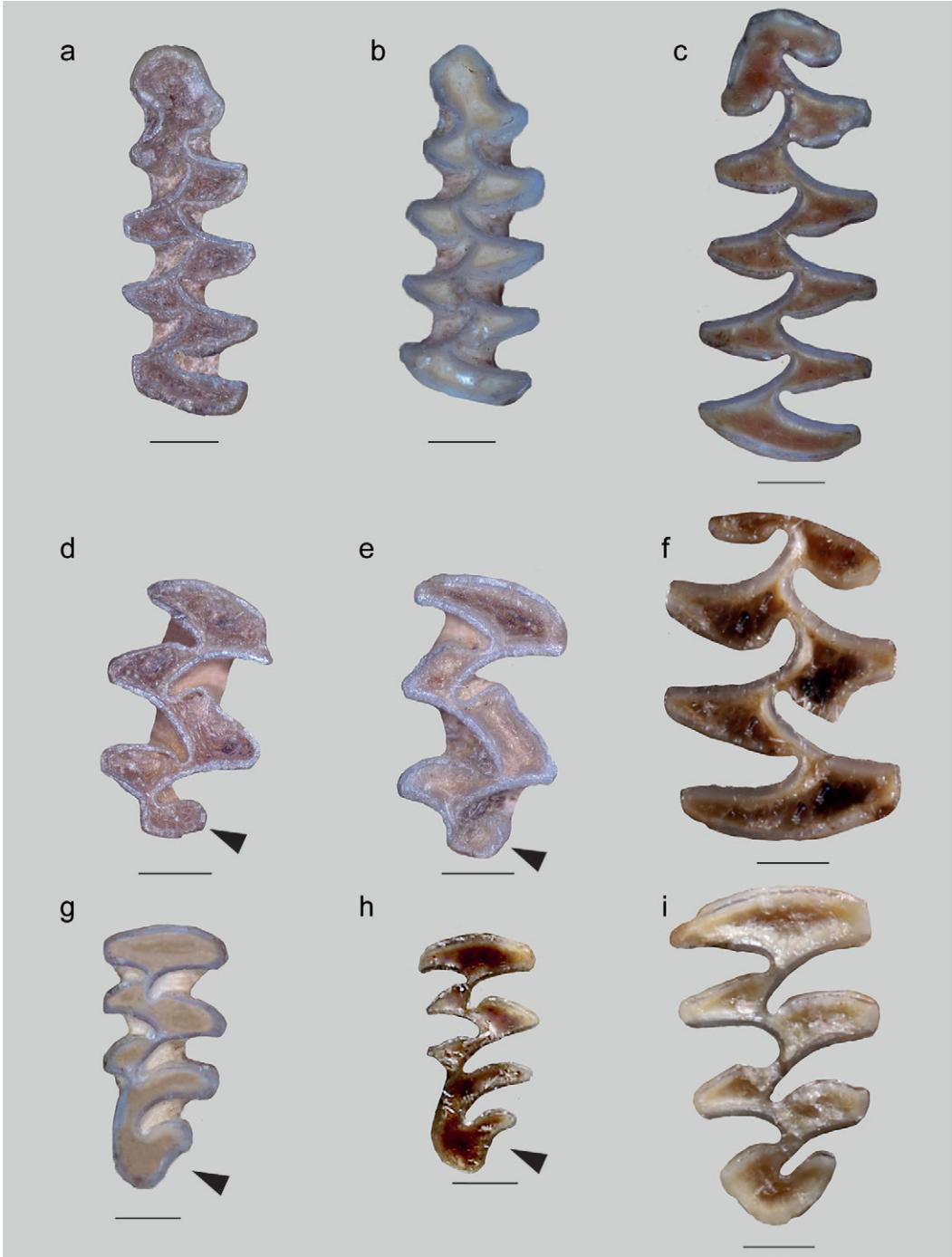
FIGURE 2. Characteristics of rodent teeth collected from Snowy Owl (*Bubo scandiacus*) pellets from Ungava Peninsula, Quebec. a and b. First lower molar of Meadow Vole (*Microtus pennsylvanicus*). c. First lower molar of Ungava Collared Lemming (*Dicrostonyx hudsonius*). d and e. Second upper molar of Meadow Vole. f. Second upper molar of Ungava Collared Lemming. g and h. Third upper molar of Meadow Vole. i. Third upper molar of Ungava Collared Lemming. Black arrows indicate the diagnostic supplementary "button shape" element in second upper molar of Meadow Vole, and the simplicity of the loop of the third upper molar of Meadow Vole. Scale bar: 1 mm. Photos: Louis Arbez.

landmark placement is automated by first standardizing the orientation of the molar by manually marking four landmarks (white circles in Figure 3a) enabling the automatic detection of 14 additional landmarks defined as extreme tips of salient and re-entrant triangles and loop tips (Navarro *et al.* 2018). GPA and principal component analyses (PCA) were performed in R version 4.0.3 (R Core Team 2020) using the "geomorph" package, version 3.2.0 (Adams *et al.* 2019). Tooth length was estimated using the Euclidean distance between landmarks 1 and 13 (Figure 3a,b).

The minimum number of individual (MNI) rodents was calculated for each pellet based on the most numerous skeletal component (i.e., left and right mandible or teeth). For example, a pellet with two left mandibles and five right mandibles has an MNI of 5.

Nine of the 10 sets of owl pellets contained small vertebrate remains that did not show a high degree of digestion and in which teeth were found (Figure 2). A total of 75 individual rodents were identified to the species level, including 65 Ungava Collared Lemmings (86.6% of the MNI) and 10 voles (*Microtus* spp.; 13.3% of the MNI; Table 1). All vole second upper molars possessed a supplementary "button shaped" element at the anterior part, no third upper molar exhibited a complex posterior loop morphology, and all second lower molars had four closed
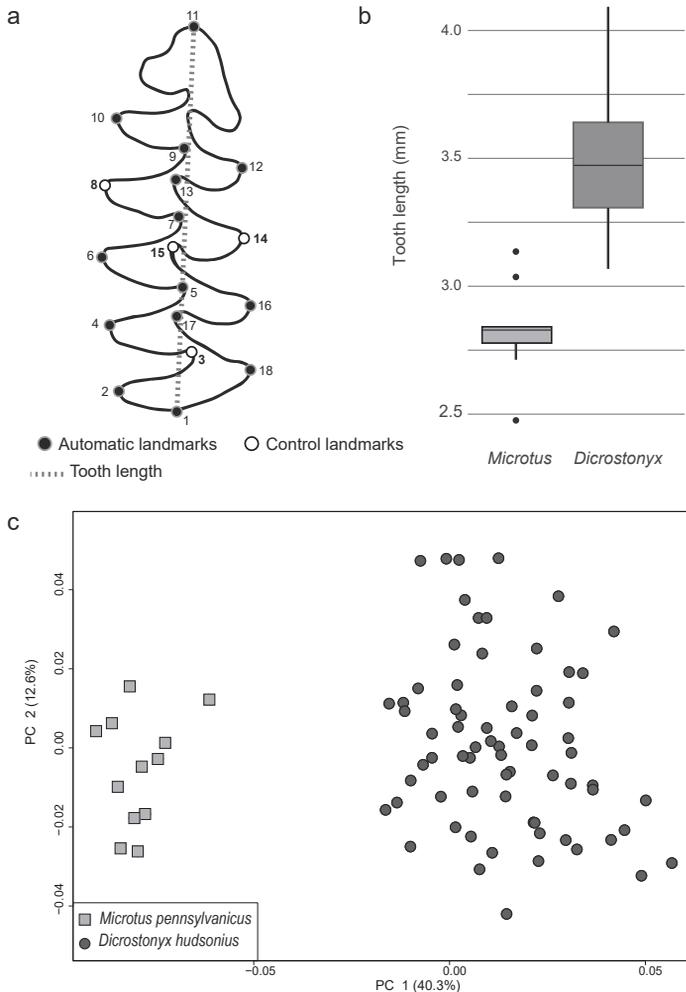

FIGURE 3. a. Landmarks for lemming (*Dicrostonyx* spp.) and vole (*Microtus* spp.) first lower molar (m1). White circles indicate manually applied landmarks, black circles are automatically detected landmarks, dotted line shows tooth length. b. Boxplot of m1 length of Meadow Vole (*Microtus pennsylvanicus*) and Ungava Collared Lemming (*Dicrostonyx hudsonius*). c. Principal component analysis (PC 1 and PC 2 planes) of Meadow Vole (*Microtus pennsylvanicus*) and Ungava Collared Lemming (*Dicrostonyx hudsonius*) m1, including percentage of shape variation explained by each PC.

triangles, indicating that they were all Meadow Voles. These two species were the only rodent remains in the owl pellets and no juvenile lemmings or voles were found.

PCA (Figure 3c) showed that the morphological distribution of the specimens from the owl pellets was not uniform (PC 1: 40.3%; PC 2: 12.6%), but fell into two homogeneous groups; this confirms the presence of two species. These two distinct groups can be identified along the PC 1 axis, one attributed to Ungava Collared Lemming on the positive side and the other to a vole species, confidently identified as Meadow Vole, on the negative side. This difference is also shown by tooth length: Ungava Collared Lemmings have longer teeth than Meadow Voles (Figure 3b). Variability of Meadow Vole tooth length (range 2.4–3.2 mm) is commonly found among adults in other populations (e.g., Wallace 2006).

The distribution range maps for North American rodents generated by Hall (1981) are widely used in many studies (e.g., Barnosky 1990; Feldhamer *et al.* 2003; Spaeth 2009; Jackson and Cook 2020). According to Hall (1981), Ungava Collared Lemming is the only lemming species inhabiting the Ungava Peninsula. Meadow Vole is widespread across North America; it occupies humid grassland, marsh, and riparian areas (Tamarin 1985) and is one of the most common *Microtus* species in subarctic taiga and tundra areas in Alaska and northern Canada (Tamarin 1985). Meadow Vole is also widespread in the south and centre of the Labrador Peninsula and its distribution is thought to be limited northward by the Ungava trough (Tamarin 1985). However, few occurrences of this species have been reported beyond this limit: two specimens in the Canadian Museum of Nature collected before 1934 (CMNMA 12572 and 12573), another individual collected near Salluit in 1954 (CMNMA 31130), and five more specimens snap-trapped by Fortin and Caron (2015). Robillard *et al.* (2013) also mentioned the presence of carcasses of Meadow Voles in Snowy Owl nests. We analysed the owl pellets collected in such nests and report once again the presence of Meadow Vole in the region. Several individuals (at least 10 of various sizes) were detected in Snowy Owl pellets, suggesting that the species is part of the owl's food web, although nearly 90% of the rodent individuals in the owl pellets were Ungava Collared Lemmings.

Will the abundance of Meadow Voles in the Ungava Peninsula increase with climate change? The species' presence has been known for some time (two specimens were found in 1934) and more specimens have been found since 2013, although few animals have been collected. In both our study and the one by Fortin and Carron (2015), Meadow Voles represented approximately 10% of the identified individuals. The Labrador Peninsula is currently experiencing the effects of climate change with the southern part of Ungava Peninsula getting dryer because of a decrease in precipitation and an increase in summer temperatures (Furgal *et al.* 2002; Barrette *et al.* 2020). These changes will most likely impact marshes and meadows, habitats sought preferentially by Meadow Voles, and could disadvantage the vole. Continuous field monitoring will increase understanding of how climate change could affect the dynamics of the Meadow Vole–Ungava Collared Lemming community in the area.

In conclusion, our results suggest that the current widely used range maps for rodents should always be interpreted with caution and the one for Meadow Vole should be revised to include the northern tip of the Labrador Peninsula, namely the Ungava Peninsula.

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Author Contributions

Conceptualization: L.A., J.-F.T., A.R., and S.M.; Methodology: L.A., J.-F.T., A.R., and S.M.; Formal Analysis: L.A., J.-F.T., A.R., and S.M.; Data Curation: L.A., J.-F.T., A.R., and S.M.; Writing – Original Draft: L.A., J.-F.T., A.R., and S.M.; Visualization: L.A., J.-F.T., A.R., and S.M.

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Diet and reproductive success of Great Horned Owl (*Bubo virginianus*) at its northern breeding limit

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Abstract

We studied the diet and reproductive success of Great Horned Owl (*Bubo virginianus*) at its northern range limit during an apparent high in the Snowshoe Hare (*Lepus americanus*) population. We performed diet analyses using images from fixed motion sensor cameras and pellet and prey remains collected at active nests, and gathered data on breeding success through camera and visual observations. Pellet data at 14 nests produced 1277 prey records consisting of 65–95% Snowshoe Hare biomass. Great Horned Owls ate 18 different prey types, with overall biomass consisting of 93% mammal, 7% bird, and less than 1% insects, frogs, and fish. The mean prey mass of 714 g ($\pm$ 34 SE) was 2–25 times the mean prey mass of studies of this species at more southerly latitudes. Camera observations showed that Great Horned Owls delivered an average of 459 g/chick/d ($\pm$ 75) throughout nesting. This was significantly ($P = 0.005$) higher than observations from Alberta, at 328–411 g/chick/d. Pellet/prey remains data showed that Great Horned Owls delivering a higher proportion of hares to their nestlings successfully raised more chicks ($\chi^2_1 = 6.3$, $P = 0.012$), highlighting the importance of this prey in the population dynamics of Great Horned Owl. In addition, we observed Snowshoe Hare removing pellets beneath nest sites, revealing an apparently undocumented bias to the use of pellet analysis.

Key words: Great Horned Owl; *Bubo virginianus*; diet; Snowshoe Hare; direct observation; pellet analysis; nest camera; Arctic; Alaska boreal forest

Introduction

Predator–prey interactions are key structuring features to many ecosystems (Gilman *et al.* 2010). In Arctic ecosystems, which are generally less productive and have strong seasonal pulses, avian predators are important in maintaining ecosystem stability via top-down controls (Ims and Fugelei 2005). However, little is known about the role of Great Horned Owl (*Bubo virginianus*) in these controls, despite it being an apex avian predator in the Arctic (Rohner *et al.* 2001).

Great Horned Owl is the most widespread year-round raptor in North America (Sibley 2014). In order to inhabit ecosystems from Arctic Alaska to Amazon jungles, Great Horned Owl must be highly adaptable to different habitat types and food sources (Bent 1961; Donázar *et al*. 1989). Although this owl typically has a generalist diet (Bent 1961), it specializes in different prey items across its range during periods of prey abundance. For example, in Minnesota and Wisconsin, Great Horned Owls consumed more Ruffed Grouse (*Bonasa umbellus*) at times of high grouse abundance (Errington 1937), while in Iowa they consumed more Ring-necked Pheasant (*Phasianus colchicus*) when pheasants were abundant (Errington 1938). In Alberta and Yukon Territory, its breeding success increased when Snowshoe Hare (*Lepus americanus*) was more abundant (Rusch *et al.* 1972; Rohner *et al.* 2001). To gain a better understanding of the interactions between this apex avian predator and abundant prey in the Arctic, we sought to estimate the composition and quantity of Great Horned Owl's diet in relation to breeding success during years of high hare abundance (3–5 hares/ha; C. Montgomerie and K.K. unpubl. data). We used a combination of traditional pellet analysis techniques (despite its known biases; Dodson and Wexler 1979) and more modern nest camera technology. Nest camera technology was recently tested in studies of raptor diet to help reduce biases in pellet analysis (Robinson *et al.* 2015) and nest cameras proved an effective tool to study the diet and breeding success of Gyrfalcon (*Falco rusticolus*) nesting on cliffs in the Arctic (Robinson 2016).

Methods

Study area

We studied Great Horned Owl diet during the spring breeding seasons of 2017–2018 along the Middle Fork Koyukuk River in Arctic Alaska roughly between latitudes 67–68°N and longitudes 149–150°W. The low elevations of the river valley are surrounded by mountainous topography of the Brooks Range. At this latitude, the boreal forest is confined to lower elevations and consists largely of Black Spruce (*Picea mariana* Miller) and White Spruce (*Picea glauca* Moench). Trees large enough to support nests tend to concentrate in drainages, creating a well-defined nesting habitat for Great Horned Owl. The area is accessible by the Dalton Highway, which parallels both the river and the Trans-Alaska Pipeline System (hereafter "the pipeline"). The study site was bounded to the north by latitudinal tree line north of Nutirwik Creek and extended ~100 km south along the Dalton Highway to Cathedral Mountain. The area lies adjacent to the southeastern border of Gates of the Arctic National Park, and includes the small communities of Coldfoot and Wiseman, Alaska.

Nest searching

Great Horned Owls do not build their own nests but typically use nests built by other raptors such as Red-tailed Hawk (*Buteo jamaicensis*) or large passerines such as Common Raven (*Corvus corax*; Bent 1961). However, in boreal forests near the latitudinal tree line, raptor diversity and density are relatively low (Marti *et al.* 1993) and tree-nesting Great Horned Owls in these northerly boreal forests often use witch's broom growths in lieu of old nests (Rohner *et al.* 2001). Witch's brooms, also known as spruce broom rust, result from infections of the fungus *Chrysomyxa arctostaphyli* affecting mainly *Picea* and *Arctostaphylos* spp. throughout North America (Nienstaedt and Zasada 1990). The infection causes Black Spruce and White Spruce throughout the boreal forest to produce branches that proliferate in clumps that can grow large enough to support an owl nest (Figure 1). All tree nests we observed in the Middle Fork Koyukuk Valley were in witch's brooms. We observed owls laying eggs directly into depressions in the witch's brooms without any apparent structure, as well as in crushed nest-like structures that could have been old raven nests.

FIGURE 1. Great Horned Owl (*Bubo virginianus*) adult and chicks nesting on a large witch's broom along the Middle Fork Koyukuk Valley, Alaska (67.8442°N, 149.8326°W), June 2017. Only pellets were collected from this nest because it could not be monitored by cameras. Photo: M. Reynolds.

We located nests using a combination of methods from Shook (2002) and Rohner and Doyle (1992). We used call surveys to locate Great Horned Owls in January and February, before owls initiated nesting (Ronher and Doyle 1992; Reynolds *et al.* 2021). After nesting began in late March–early April, we continued to use call surveys and conspecific broadcasts to elicit responses during the day and night following Rohner and Doyle (1992). When Great Horned Owls responded to playback, we used ArcGIS (ESRI 2017) to triangulate their location (Rohner and Doyle 1992). We used systematic daytime searching on foot to locate nests within ~200 m radius of the triangulated location (Rohner and Doyle 1992; Shook 2002). During these daytime nest searches, we examined all potential nest platforms for signs of occupation such as bone fragments, feathers, Snowshoe Hare feet, pellets, prey remains, and owl feathers stuck to branches. The best indication of occupation was the presence of down feathers on the outside of a nest.

Nest monitoring

We visited nests every two weeks, noting occupation, which adults were present, and number of chicks. Motion sensor cameras were deployed to monitor diet, hatch, and fledging dates between our visits at half the nests we monitored (see below). Great Horned Owls typically start "branching" (leaving the nest before capable of flight) 45–49 d after hatch (Hoffmeister and Setzer 1947). Thus, we define fledging date as the date when chicks start branching, regardless of their ability to fly.

Where possible, we deployed motion sensor cameras (Reconyx Hyperfire PC900, Holmen, Wisconsin, USA) at nests to collect diet information (*n* = 7). We set all nest cameras to take three rapid-fire pictures with each trigger on medium/high sensitivity. To conserve battery power as chicks became continually active in the nest from hatch until fledge, we set a quiet period of 30 s between triggers. Nest cameras used an infrared illuminator to take pictures at night with the balanced night mode setting. We attached nest cameras to the pipeline and trees using bungee cords rated for –40°C. We set a back-up camera on each nest that took two pictures per trigger and allowed us to identify prey items from different angles.

We followed Robinson's (2016) recommendations of placing cameras 1–2 m laterally and 1 m above the nest. Unlike Gyrfalcon in Robinson's (2016) study that nested on cliffs, Great Horned Owl in the Middle Fork Koyukuk Valley nested on a variety of structures (e.g., pipeline supports, trees, and cliffs). We were able to place cameras on all five pipeline nests (Photos S1, S2, S3, S4), two of eight tree nests, but not on the single cliff nest due to an unstable cliff face. We were not able to place cameras on tree nests when the nest tree and surrounding trees were unable to support a climber. Thus, out of the 14 nests we monitored (*n* = 7 in 2017, *n* = 7 in 2018), we placed cameras on seven (*n* = 4 in 2017, and *n* = 3 in 2018), four of which hatched (*n* = 2 in 2017, *n* = 2 in 2018). Three of the nests observed were occupied both years of the study. Cameras were removed after nestlings fledged by the end of June.

Collection of pellets and prey remains

We collected pellets and prey remains at all 14 nests to compare the accuracy of pellets and nest cameras in providing the most complete picture of diets and to gather standardized diet information on nests not equipped with a camera. Upon finding a nest, we collected all pellets and prey remains in the surrounding area to ensure that future pellets collected were deposited between known collection dates (Shook 2002), and biweekly thereafter.

Prey identification

We analyzed the prey composition and biomass using both pellet/prey remains and nest cameras. We used nest camera photos to identify prey consumed at nests to the lowest possible taxonomic level (Nielsen 1999), then assigned average mass values of species based on references for birds (Sibley 2014), mammals (Kays and Wilson 2009), amphibians (Stebbins 2003), fish (Wootton 1998), and insects (Collet 2010). Because small rodents can be difficult to identify using photographs, we combined all rodents weighing less than 100 g into the category "microtine".

Pellets and prey remains were grouped by collection date and nest site, wrapped in heavy duty aluminum foil, and dried/sanitized in a standard oven at 165°C for 45 min. We counted the most frequently occurring bone of each species per collection to avoid double-counting prey (Nielsen 1999). Again, we identified prey to the lowest possible taxonomic level and combined all rodents weighing less than 100 g into the category "microtine" to be consistent with nest camera methods and assigned average mass values of species using references listed above. We also used MacDonald (2003) and Scott and McFarland (2010) to identify remains of small mammals and birds from pellets. To assign biomass of immature prey in analyses of both nest cameras and pellets/prey remains, we visually estimated the prey's size as a proportion of adult size then applied this proportion to the average biomass value of the species (Robinson 2016).

We used a Poisson regression to examine the relationship between fledging success and the proportion of hare biomass in the diet at all nests. Values reported are means ± SE. Alpha levels for significance testing was set to 0.05 and computed using R statistical software (R Core Team 2013).

Results

Diet composition

Nest cameras on seven nests captured up to 40 000 photos each, documenting 258 prey items and 12 different prey types, with an estimated total of 171 kg of prey consumed. Pellets and prey remains from these same seven nests revealed 138 prey items and 11 different prey types with an estimated 94 kg of prey consumed. Pellets and prey remains collected from a total of 14 nests, including the seven nests without cameras, yielded 215 prey items from 14 different prey types, with an estimated total mass of 170 kg of prey consumed. Altogether, cameras and pellets/prey remains revealed a total of 18 different prey types.

Both nest cameras (Photo S3) and pellets/prey remains identified Snowshoe Hare as the largest component in the diet with an average of 93% and 91% of total biomass, respectively (Figure 2). Of this hare biomass, 85% and 88% came from adult hares for cameras and pellets/prey remains, respectively. Pellets were collected at all nests and showed little difference in the proportion of hare biomass in the diet between 2017 (90 ± 8%) and 2018 (91 ± 7%).

Based on camera data, the items that contributed most biomass to the diet after hares were Muskrat (*Ondatra zibethicus*; 2.5%), microtine rodents (2.0%), birds (1.5%), and other (1.6%). Birds identified in images were Mallard (*Anas platyrhynchos*), Green-winged Teal (*Anas crecca*), Spruce Grouse (*Canachites canadensis*), Canada Jay (*Perisoreus canadensis*), Dark-eyed Junco (*Junco hyemalis*), and a sandpiper (*Calidris* sp.). Prey items in the camera data comprising the "other" category were Red Squirrel (*Tamiasciurus hudsonicus*), Wood Frog (*Lithobates sylvaticus*), dragonfly (Odonata), and six small (<350 g) unidentified mammalian prey (Table 1).

From the pellet/prey remains data, the items that contributed most biomass to the diet after hares were birds (7.3%), microtine rodents (1.1%), and other (0.6%). Birds identified in pellets/prey remains were Mallard (3.2%), Spruce Grouse (1.9%), and Willow Ptarmigan (*Lagopus lagopus*; 1.3%), with Northern Hawk Owl (*Surnia ulula*), Green-winged Teal, Canada Jay, and small passerines making up the remaining 0.8%. The "other" category was comprised of Red Squirrel, Ermine (*Mustela erminea*), carabid beetles, a small fish, and small pieces of Moose (*Alces americanus*) fur indicative of scavenging (Table 1).

Provisioning rates

We used camera data to calculate the daily provisioning rate. Of the seven nests equipped with cameras, only four hatched (*n* = 2 in 2017, *n* = 2 in 2018). From these four nests, the average post hatch provisioning rate was 1304 g/d (± 209), or 459 g/chick/d (± 76). Provisioning rates increased over time in all but Nest 2, where it decreased slightly (Figure 3). Dramatic increases in g/chick/d corresponded with chick mortalities in Nests 1 and 3, when nest occupancy decreased from three to two chicks (Figure 3).

Diet and nesting success

Of the 14 nests monitored during the study, four failed to hatch. Of the four failed nests, two succumbed to predation by Common Raven (Photo S5) and two failed for unknown reasons, where intact eggs were found on the snow below the nest. Of the 10 nests that hatched, each fledged 1–3 chicks (average 1.4 ± 0.5 chicks/nest) in both 2017 and 2018. We used pellet/prey remains information collected at all 14 nests to compare the diet at each nest to fledging success. The average proportion of hare biomass in the diet was 85% (± 6) across both years. Hare biomass in the diet varied among nests. Four nests had ≥95% hare biomass, one nest had 85–95% hare biomass, five nests had 75–85% hare biomass, and three nests had 65–75% hare biomass. One nest failed before we could gather adequate diet information. A likelihood ratio test showed a significant positive relationship (χ^2_1 = 6.3, P = 0.012) between fledging success and the proportion of hare biomass in the diet at all nests, where nestlings consuming a greater proportion of hares were more likely to fledge (Figure 4).
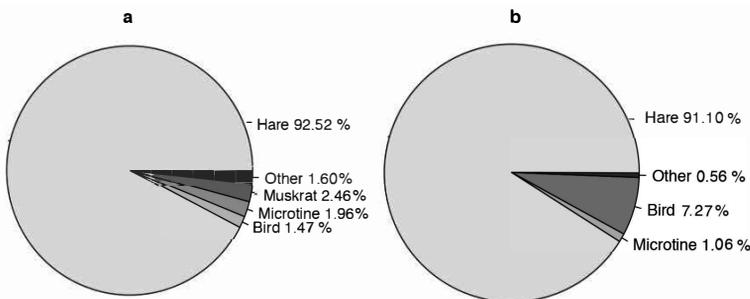

FIGURE 2. Composition of the diet of nesting Great Horned Owl (*Bubo virginianus*) as captured through the use of fixed motion sensor cameras (a) and pellet/prey remains analysis (b) in the Middle Fork Koyukuk Valley, Alaska, USA in 2017–2018.

TABLE 1. Number of each prey type observed, the method of observation (nest camera or pellet/prey remains collection), the total estimated mass of each prey type, and proportion of the total diet consisting of each prey type in the diet of nesting Great Horned Owl (*Bubo virginianus*) in the Middle Fork Koyukuk Valley, Alaska, during the breeding seasons of 2017–2018.

Prey type		Method of observation					
		Camera (*n* = 7 nests)			Pellets (*n* = 14 nests)		
Prey Type	Avg. weight (g)	Min. no. of items	Total weight (g)	% Total mass (g)	Min. no. of items	Total weight (g)	% Total mass (g)
Hare	750–1360	124	158 270	93	116	154 710	91
Microtine	30	112	3360	2	60	1800	1
Muskrat	1400	3	4200	2	0	0	0
Squirrel	340	2	680	<1	2	680	<1
Unknown	340	6	2040	1	0	0	0
Ermine	588	0	0	0	1	258	<1
Birds	27–1100	8	2507	1	31	12 350	7
Frog	8	2	16	<1	0	0	0
Dragonfly	1	1	1	<1	0	0	0
Beetle	1	0	0	0	3	3	<1
Fish	20	0	0	0	1	20	<1
Moose	270 000–600 000	0	0	0	1	1	0
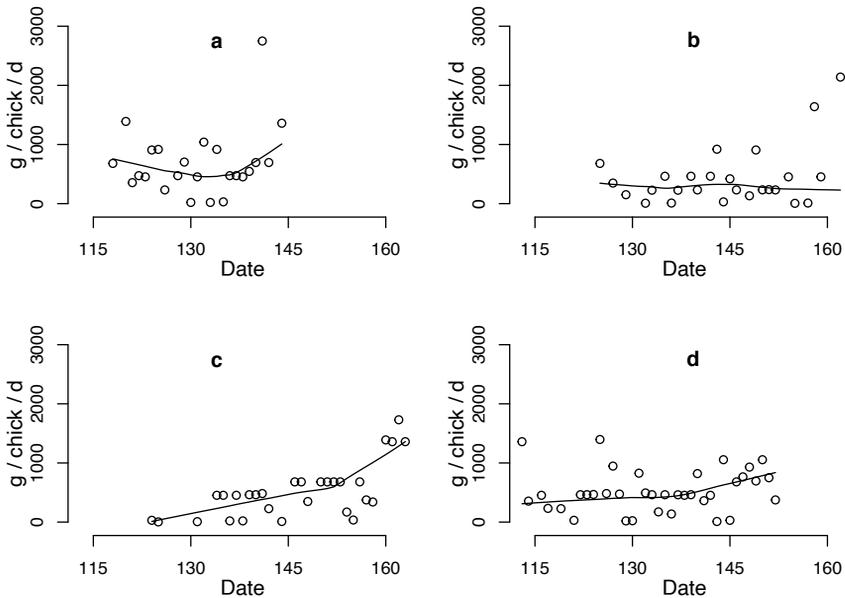
FIGURE 3. Specific food provisioning rates (g/chick/d) to Great Horned Owl (*Bubo virginianus*) chicks between hatch and fledge, based on nest cameras in the Middle Fork Koyukuk Valley, Alaska, USA (2017–2018). Lowess curves show general trends in data. Dates are in day of year. Nest 1 (a) fledged two chicks in 2017. Nest 2 (b) fledged three chicks in 2018. Nest 3 (c) fledged two chicks in 2017. Nest 4 (d) fledged three chicks in 2018.

Discussion

Nests proved to be more difficult to find in Arctic boreal forests than the mixed and deciduous forests at lower latitudes (Rohner and Doyle 1992; Little and Little 2018), leading to a small sample size of nests (*n* = 14). Half of these nests were also monitored using cameras. Using two methods allowed us to compare diets identified by each; supplementary cameras also showed a previously undocumented potential bias in pellet analysis in the boreal forest when Snowshoe Hares are present.

Unlike previous studies of raptor diet in the Arctic (Longland 1989; Shook 2002; Eisaguirre 2015; Robinson 2016), pellets in our study accumulated under

FIGURE 4. Relationship ($\chi^2_1 = 6.3$, $P = 0.012$) between fledging success and Snowshoe Hare (*Lepus americanus*) biomass in diet of Great Horned Owl (*Bubo virginianus*) based on pellet/prey remains at their northern breeding limit in the Middle Fork Koyukuk Valley, Alaska, USA, 2017–2018.

nests at lower than expected rates. Most pellets deposited below nests disappeared quickly, leaving mainly large prey remains. To investigate this observation, we deployed motion sensor cameras ~5–10 m away from nest trees, facing the trunk and observed that most pellets were removed or consumed by Snowshoe Hare (Photo S6) and Red Squirrel. We observed hares below owl nests on 148/170 observation days (average of ~8 times per day) while Red Squirrels were observed on 81 of the same observation days (average one visit per day). Based on meal to pellet intervals (Marti 1969), we assumed that each Great Horned Owl older than seven days old casts about one pellet per day (Houston *et al.* 2013). At only one nest, a cliff nest where pellets fell onto a lower outcropping unreachable by squirrels or hares, did we collect the expected number of accumulated pellets. However, during most pellet collections, we found less than a quarter of the expected pellets.

Poor winter nutrition may be driving hares and squirrels to supplement their diet with the undigested bone, feathers, fur, and carbohydrate residues found in owl pellets. The carbohydrate residues from pellets may contain seeds, cellulose, and chitin from prey stomachs (Houston *et al.* 2013), and osteophagy was observed in several other herbivores for dietary phosphorus and calcium (Denton *et al.* 1986). Further study is needed to determine if owl pellets are a significant nutritional supplement for hares and squirrels in boreal forests.

Pellets versus cameras for estimating diet

Data from pellets/prey remains and cameras showed similar results, however camera data captured greater detail. Cameras recorded events as they occurred, while cameras acted as biweekly summaries. Pellets/

prey remains revealed six types of prey that cameras did not, while cameras captured four types of prey not seen in pellets. Because cameras were placed only at half of the nests where pellets were collected, it is possible that the six prey types not captured by cameras could have been observed if all nests had been equipped with cameras. Nest cameras also captured behavioural data, including dates of hatch, fledge, and failure, as well as successful and attempted nest predation by Common Ravens.

Although nest cameras provided more diet detail than pellets/prey remains, they were logistically feasible at fewer nests. All cameras positioned 1–2 m from the nest as recommended by Robinson (2016) successfully captured photos throughout the nesting period. However, cameras positioned farther from the nest did not trigger reliably and were not included in our analysis. In most cases, we were unable to use cameras for nests in witch's brooms, making pellets the only feasible option for analyzing diet of most tree nesting pairs. Another potential difference exists if Great Horned Owl pairs that nest on pipeline structures have a different diet than natural tree nesters.

Diet and breeding success

We estimated that adults delivered an average of 459 g/chick/d (± 76) from nest camera data. Previous studies in Alberta showed a lower average of 328–411 g/d during high hare abundance (McInvaille and Keith 1974). Because the study in Alberta collected pellet/prey remains every other day, the larger daily provisioning of prey we observed could be due to the different dietary analysis methods. The unexpected disappearance of pellets around nests and our bi-weekly as opposed to every other day pellet collections precludes a direct comparison using pellet analyses.

Although Great Horned Owls often display a generalist diet, other studies highlight their increased dependence on particular prey species during times that species is abundant. Results of our study confirm the direct link between the abundance of Great Horned Owl and Snowshoe Hare (Rohner *et al.* 2001), where we found that owls consuming a greater proportion of hare biomass fledged significantly more chicks. During hare peaks in Alberta and Yukon, hares composed 90–98% and 75–97% of the Great Horned Owl's winter diet biomass, respectively (Adamcik *et al.* 1978; Rohner 1995). Hares composed a similar proportion of the Great Horned Owl's biomass in our study: 65–99%.

Adamcik *et al.* (1978) and Rohner (1995) also studied Alberta and Yukon owl populations during lows in the local hare populations and observed that in low hare years, hares composed only 16% and 13% of the Great Horned Owl's diet biomass, respectively. The northernmost breeding population we studied

should also be examined during years of hare scarcity to better quantify the importance of hares in the Great Horned Owl's breeding ecology throughout the hare population cycle.

The proportion of mammal biomass in the Great Horned Owl diet was consistent with other studies across North America (93%; Cromrich *et al.* 2002). However, mean prey size in our study was 2–25 times greater than previous studies. Mean prey sizes recorded by others in California, Idaho, Washington, and Chile ranged from 28 to 266 g (Fitch 1947; Rudolph 1978; Jaksic and Yañez 1980; Marti and Kochert 1996). Mean prey size in our study was 616 g for cameras and 714 g for pellets/prey remains.

Although a literature review by Houston *et al.* (2013) showed that chicks leave the nest 42 d after hatch, we found that chicks branched out as early as 28 d after hatch. Chicks stayed in the nest for 42 d in only one nest where exact hatch dates were known. The average time between hatch and branching in our study was 36 d (± 4). The greater mean prey size (616–714 g) and daily provisioning (459 g/chick/d) compared to other studies might explain why chicks developed faster and were able to leave the nest earlier in our study.

Witch's brooms

Little information on the ecology of witch's brooms has been published, yet they appear attractive to many species in boreal forests. We observed four other species nesting in witch's brooms including Common Raven, Northern Goshawk, Merlin (*Falco columbarius*), and American Kestrel (*Falco sparverius*). We saw eight species visiting witch's brooms frequently including Yellow-rumped Warbler (*Setophaga coronata*), Spruce Grouse, Boreal Chickadee (*Poecile hudsonicus*), White-crowned Sparrow (*Zonotrichia leucophrys*), Varied Thrush (*Ixoreus naevius*), Grey-cheeked Thrush (*Catharus minimus*), American Marten (*Martes americana*), and Red Squirrel. Additionally, Shook (2002) found a Northern Hawk Owl nesting in a witch's broom in our study area, and several more throughout interior Alaska. Future studies of witch's brooms could reveal possible symbiotic relationships between *C. arctostaphyli* and the many species that use their manifestations. This fungus may play an unsung role in boreal ecosystems that may prove important in future conservation efforts.

Author Contributions

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

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Supplementary Materials:

Photo S1. Adult Great Horned Owl (*Bubo virginianus*) triggers nest camera placed on Trans-Alaska Pipeline nest near Coldfoot, Alaska, while three chicks watch from the nest, June 2018.

Photo S2. Adult Great Horned Owl (*Bubo virginianus*) broods three chicks in a nest along the Trans-Alaska Pipeline near Coldfoot, Alaska, May 2018.

Photo S3. An adult Great Horned Owl (*Bubo virginianus*) delivers a Snowshoe Hare (*Lepus americanus*) to chicks in a nest on the Trans-Alaska Pipeline near Coldfoot, Alaska, May 2018.

Photo S4. Common Raven (*Corvus corax*) visits Great Horned Owl (*Bubo virginianus*) nest on the Trans-Alaska Pipeline near Coldfoot, Alaska.

Photo S5. Common Raven (*Corvus corax*) steals an egg from Great Horned Owl (*Bubo virginianus*) nest in witch's broom, May 2018, likely the northernmost Great Horned Owl nest on record at 68.0113°N, 149.7345°W.

Photo S6. A camera placed on the ground beneath Great Horned Owl (*Bubo virginianus*) nest shows Snowshoe Hare (*Lepus americanus*) removing an owl pellet shortly after it was cast, June 2018, at 67.8442°N, 149.8326°W.

Assessing migration strategies and cause specific mortality of adult female White-tailed Deer (*Odocoileus virginianus*) in North Dakota, USA

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Abstract

Life-history characteristics of White-tailed Deer (*Odocoileus virginianus*) have been documented in areas of the Northern Great Plains, but limited information is available in grassland dominated regions. We documented migration strategy, home range use, and survival of adult female White-tailed Deer in central North Dakota. We monitored 62 radio-collared adult (>1.5 year-old) female White-tailed Deer from February 2010 to December 2012. We documented 86 summer home ranges and classified deer as resident, migratory, or exhibiting a late season movement. Mean migration distance between non-overlapping summer and winter home ranges was 11.76 km (SE 0.86, $n = 21$). Mean late season movements were 20.69 km (SE 2.94, $n = 7$) and were likely the result of deer exhausting food resources throughout winter. We also developed five competing models that represented variation in survival among time periods (e.g., pre-hunt, hunt, and post-hunt in 2010 and 2011). Our top model indicated that survival (S) was similar between hunt 2010 and post-hunt 2011 periods but was lower (S = 0.82; SE 0.04, 95% CI 0.73–0.89) than the remaining time periods (S = 0.97; SE 0.01, 95% CI 0.93–0.99). Our results suggest that deer migration strategies and survival are likely influenced by a combination of winter severity and food availability. Mortalities attributed to hunter harvest were low during our study, which may indicate that increased recreational opportunities could be made available, even after severe winters.

Key words: Migration; mortality; Northern Great Plains; *Odocoileus virginianus*; survival; White-tailed Deer

Introduction

White-tailed Deer (*Odocoileus virginianus*) were historically limited to bottomland hardwoods, riparian forests, and lacustrine woodlands that punctuated the landscape of North Dakota (Knue 1991). Deer radiated from these habitats with conversion of grasslands to agriculture (Dusek *et al.* 1989; Heffelfinger 2011), suppression of fire that allowed encroachment of trees in prairie environments (Oehler *et al.* 1995), predator management (VerCauteren and Hygstrom 2011), and regulations that closed hunting seasons to manage populations (Knue 1991). Presently, White-tailed Deer occur throughout the state; however, factors thought to limit the species include severe winter weather, predators (i.e., Coyotes [*Canis latrans*]; Grovenburg *et al.* 2011a), and human modification of suitable habitats. Previous studies in the Northern Great Plains documented movement patterns and home range size (Sparrowe and Springer 1970; Brinkman *et al.* 2005; Smith *et al.* 2007; Grovenburg *et al.* 2009), and survival (Brinkman *et al.* 2004; Smith *et al.* 2007; Grovenburg *et al.* 2011a) of White-tailed Deer.

White-tailed Deer at northern latitudes are classified as residents (do not migrate but may shift habitat use within range in response to environmental conditions) or migrators; migrators can be either obligate (migrate a single time for the duration of the season and each season thereafter) or conditional (migrate some seasons but not others, or temporarily migrate for <1 month; Sabine *et al.* 2002; Fieberg *et al.* 2008; Grovenburg *et al.* 2011b). Seasonal movement patterns at northern latitudes include short distance, dispersal, and seasonal migration (Kernohan *et al.* 1994; Brinkman *et al.* 2005). Short distance movements typically occur under mild winter conditions when

food resources are sufficient (Marchinton and Hirth 1984; Grovenburg *et al.* 2009). Seasonal migration from winter to summer home ranges is the most commonly documented movement pattern of White-tailed Deer at the northern limits of their range (Ozoga and Gysel 1972; Nelson 1998; Van Deelen *et al.* 1998). In the Northern Great Plains, mean migration distance between seasonal ranges generally exceeds 10 km (Brinkman *et al.* 2005; Smith *et al.* 2007; Grovenburg *et al.* 2009).

Radio telemetry studies conducted throughout the Northern Great Plains suggest environmental and anthropogenic factors influence White-tailed Deer survival on a regional level (Brinkman *et al.* 2004; Grovenburg *et al.* 2011a; Robling 2011). Causes of adult deer mortality in northern climates include hunting, vehicle collisions, illegal harvest (Dusek *et al.* 1992; Brinkman *et al.* 2004; Grovenburg *et al.* 2011a), severe winter weather (DelGiudice *et al.* 2002), predation (Mech 1984; Van Deelen *et al.* 1997; Whitlaw *et al.* 1998), starvation (Lamoureux *et al.* 2001), and disease (Matschke *et al.* 1984). Most studies indicate hunter harvest as the primary cause of adult mortality, which emphasizes the need for accurate harvest mortality rates for proper management (DelGiudice *et al.* 2002).

Although White-tailed Deer ecology has been studied extensively in South Dakota (Sparrowe and Springer 1970; Kernohan *et al.* 1994; Burris 2005; Grovenburg *et al.* 2009; Robling 2011) and western Minnesota (Brinkman *et al.* 2005; Swanson 2005), limited information exists in North Dakota where latitudinal variation in climate and limited winter cover likely influence seasonal movements, home range size, and survival. Previous research addressing these factors in North Dakota focussed on wildlife management areas (WMA) where supplemental food plots were available throughout winter (Jensen 1999; Smith *et al.* 2007). Our objectives were to document seasonal movement patterns and home ranges while assessing how mortality varies during the recreational hunting season compared to other time periods for White-tailed Deer on the Missouri Coteau of central North Dakota, USA.

Study Area

We monitored adult female White-tailed Deer in the Wing-Tuttle Study area (Burleigh, Kidder, and Sheridan counties; 47.1408°N, 100.2790°W) in central North Dakota from 2010 to 2012. These counties were located within the Northwestern Glaciated Plains Level III Ecoregion (Bryce *et al.* 1998) and comprised an area of 10 558 km². Grasslands were the dominant habitat type and comprised 57.7% of the landscape. Croplands comprised 26.7%, wetlands

and water comprised 11.3%, developed land 4.1%, and other land uses comprised <1% of the total landscape (USDA 2011). There were 17 599 ha classified as wildlife management areas (WMAs), 13 293 ha as National Wildlife Refuges, and 12 821 ha as waterfowl production areas (WPAs; C. Penner pers. comm. 15 June 2021) within these three counties. Mean long-term (1981–2010) summer temperature was 19.4°C and mean long-term (1981–2010) annual precipitation was 44.9 cm (North Dakota Office of Climatology 2012).

Native vegetation included Western Wheatgrass (*Pascopyrum smithii* Barkworth & Dewey), Big Bluestem (*Andropogon gerardii* Wipff), Little Bluestem (*Schizachyrium scoparium* Nash), Needle-and-thread (*Hesperostipa comata* Trinius & Ruprecht), Green Needlegrass (*Nassella viridula* (Trinius) Barkworth), Prairie Cordgrass (*Spartina pectinate* Link), Northern Reedgrass (*Calamagrostis stricta* Timm), Plains Muhly (*Muhlenbergia cuspidata* Torey & Hooker), Prairie Junegrass (*Koeleria macrantha* Ledebour), Blue Grama (*Bouteloua gracilis* Kunth & Lagasca), and Inland Saltgrass (*Distichlis spicata* Torrey; Johnson and Larson 1999). Regional cultivated crops included wheat, sunflowers, corn, soybeans, canola, flaxseed, barley, peas, oats, dry beans, potatoes, sorghum, triticale, millet, rye, lentils, mustard, and safflower (USDA 2011).

Methods

Data collection

We captured and radio-collared adult female deer (>1.5 years old) using helicopter net guns (February 2010; Jacques *et al.* 2009) and modified Clover traps (winter 2010–2011; Clover 1954). We restrained, blindfolded, processed, and released each deer at capture sites. We fitted very high frequency (VHF) radio-collars (model V5C 176; Sirtrack, North Liberty, Iowa, USA) to each captured deer; radio-collars were equipped with mortality sensors that switched to mortality mode after the transmitter remained stationary for ≥8 h.

We monitored adult radio-collared deer 2–3 times per week from 16 February 2010 to 30 December 2012 using a combination of aerial telemetry from a fixed-winged aircraft (American Champion 8-GCBC Scout, Burlington, Wisconsin, USA) and ground telemetry. We did not locate individuals on successive days or at similar times of day during the same week to ensure we accurately characterized home ranges while minimizing autocorrelation and temporal bias in location data. We used omnidirectional antennas and hand-held 4-element Yagi antennas (Advanced Telemetry Systems, Isanti, Minnesota, USA) to visually locate individuals and perform

ground triangulation. We recorded universal transverse mercator (UTM) coordinates using a geographical positioning system (GPS) unit (Garmin III Plus, Olathe, Kansas, USA) in the aircraft during aerial telemetry flights; there was no telemetry error associated with these visual sightings. We obtained a minimum of three directional bearings using a compass from prerecorded stations. We entered bearings and stations into LOCATE III (Nams 2006) to estimate locations and error polygons. We excluded locations that exhibited 95% error ellipses ≥20 ha from further analyses to maintain consistency with other regional studies (Brinkman *et al.* 2005; Burris 2005; Grovenburg *et al.* 2009). Due to lack of roads and substantial topography within the study area, we approached most collared animals on foot to obtain visual locations so we did not determine measurement error for ground triangulation.

We investigated all mortalities to establish cause of death; however, if we could not determine cause of death in the field and carcasses were not scavenged or in an advanced state of decay, we transported them to the North Dakota Game and Fish Wildlife Laboratory in Bismarck, North Dakota for further investigation. Adult mortalities that occurred within 26 days postcapture were not included in our analyses regardless of ultimate cause of death (Beringer *et al.* 1996).

Statewide hunting seasons for White-tailed Deer were open from 3 September to 2 January 2010–2011 and 2 September–8 January 2011–2012. Hunting seasons included youth firearm, firearm, muzzleloader, and archery. Given the firearm seasons (5–21 November 2010 and 4–20 November 2011) generally exhibit the greatest hunter participation and subsequent pressure on deer (Jensen *et al.* 2011, 2012), we avoided further disturbing deer and hunters to minimize our effects on movements of radio-collared animals during the firearm hunting season; thus, reducing any potential bias-related movements. We located radio-collared deer via aerial telemetry twice during each firearm season. Flights occurred the first Monday immediately following the firearm season opener and again during the second weekend of the season. After we obtained locations, we determined land ownership inhabited by radio-collared deer. We then contacted private landowners and obtained information on hunter access to their property. We classified the following land management types into two classes (open or closed to hunting): private land open to hunting, private land closed to hunting, public (WMAs, WPAs) lands (open to hunting), and National Wildlife Refuges (closed to hunting). We did not obtain the number of hunters accessing each property.

To assess potential relationships between winter severity and migration strategies, we calculated deer winter severity indices (DWSI; Brinkman *et al.* 2005) for the Wing-Tuttle study area during the winters of 2009–2010, 2010–2011, and 2011–2012. We also calculated historical DWSI from 2001 to 2009 for comparative purposes. We obtained weather data from the North Dakota Office of Climatology (2012) and assigned one point for each day the mean temperature was ≤−7°C and an additional point for each day snow depth was ≥35.0 cm from November through March (Brinkman *et al.* 2005). We then summed the daily point accumulation for each day to calculate an annual DWSI. We considered indices <50 as mild, 50 to 100 moderate, 101 to 200 as severe, and >200 very severe winters (W. Jensen unpubl. data).

Home ranges and movements

We used the fixed-kernel method in Home Range Tools (HRT) for ArcGIS 9.3 (ESRI, Redlands, California, USA; Rodgers *et al.* 2007) to calculate 95% and 50% (core) home ranges. We used least-squares cross-validation to estimate the smoothing parameter and constructed home ranges using a minimum of 28 locations, which is sufficient for home range analyses (Seaman *et al.* 1999). Due to inaccessibility during winter months, we collected an insufficient number of locations to generate winter home ranges of individuals. Therefore, after calculating summer home ranges we classified movement types on an annual basis to assess if movement strategies differed between years of varying winter severity by using a k-means cluster analyses on individual deer locations using Euclidean distance (coordinates of deer locations; Boulanger *et al.* 2006). This analysis identified deer with two significant, non-overlapping clusters and classified them as migrators (i.e., two separate seasonal home ranges with the initial movement to an individual's winter home range occurring before 1 January). We chose 1 January as the cutoff because of the requirements of the statistical analysis combined with most deer having moved to wintering areas by this time (Smith 2005). We did not classify deer as migrators if we detected any overlap between summer and winter home ranges (Brinkman *et al.* 2005). Furthermore, we lacked sufficient data to further classify migrators as obligate or conditional. We classified deer as residents if they failed to move between separate seasonal home ranges (i.e., single cluster). We classified deer as late season migrators if they failed to migrate during a documented migratory period (single cluster) but made late-winter movements (outside 95% home range contours) of short duration (1–2 weeks) after 1 January. We compared home range estimates between years at the population level using *t*-tests and among movement classifications using analysis of variance (ANOVA) in SAS (version 9.3; SAS Institute Inc. 2011). We compared migration distance

among years using a *t*-test and considered differences significant at α = 0.05. Some animals were collared in both years but we had insufficient sample sizes to test for year effects, so we pooled data across years, even though it is understood that annual variation may exist (Schooley 1994).

Survival rates

We calculated annual and seasonal survival rates using known fate models adapted for staggered entry in program MARK (version 6.0; Pollock *et al.* 1989; White and Burnham 1999). We constructed five models incorporating variation of adult survival between and among three periods; post-hunt (January–May), pre-hunt (May–September), and hunt (September–January) and between years (Table 1). We used AIC$_c$ to select models best describing the data (Burnham and Anderson 2002). We considered models within 2 ΔAIC$_c$ from the top model as competing and used Akaike weights (w_i) to indicate model support (Burnham and Anderson 2002).

Results

We captured and radio-collared 62 adult female (>1.5 year-old) deer using helicopter net guns ($n = 48$) and Clover traps ($n = 14$). Two capture related mortalities occurred during helicopter net-gunning operations in 2010. We collected 5603 locations from the radio-collared deer. Average annual DWSI in the Wing-Tuttle study area for the winters of 2009–2010, 2010–2011, and 2011–2012 was 166 (severe), 215 (very severe), and 93 (moderate), respectively (Figure 1).

We assigned 86 classifications to 62 captured deer (some individuals were radio-collared for both years). We determined 36 (84%) of the deer were residents (overlapping seasonal home ranges) and seven (16%) were migrators (non-overlapping seasonal home ranges) during 2010 with a mean migration distance of 11.6 km (SE 1.8). During 2011, 22 (51%) deer were residents and 14 (33%) were migrators with a mean migration distance of 11.9 km (SE 1.0). Mean migration distance did not differ between years (t_{19} = −0.16, P = 0.874); mean migration distance from

2010 to 2011 was 11.8 km (SE 0.9, $n = 21$). Additionally, during winter 2011, seven (16%) radio-collared animals made late season movements; mean distance travelled was 20.7 km (SE 2.9). Number of locations during 2010 and 2011 ranged from 10 to 128 per individual collared deer. Based on visual evidence at the site, all seven late season movements resulted in radio-collared individuals leaving a habitat with no food or a depleted food source.

We calculated 86 individual summer home ranges using a mean of 49.4 locations (SE 1.0) from which we documented 58 home ranges of resident deer, 21 home ranges of migrating deer, and seven home ranges of deer that performed late season movements. Mean 50% and 95% home range size differed ($t_{56} ≤ −2.89$, $P ≤ 0.005$) by year for resident deer but not for migrating deer (mean 50%: $t_{19} = 0.10$, $P = 0.921$; mean 95%: $t_{19} = −0.11$, $P = 0.914$). Mean 50% and 95% home ranges were larger for resident deer in 2011 (2.0 km², SE 0.4; 9.5 km², SE 1.6) than 2010 (1.0 km², SE 0.1; 5.2 km², SE 0.6). Mean 50% ($t_6 = −1.49$, $P = 0.161$) and 95% ($t_6 = −1.49$, $P = 0.310$) summer home ranges for deer classified as late season movers did not differ between years.

We observed similar patterns of distribution of radio-collared deer on lands accessible to hunters in both years. During the 2010 firearms season, 80% of radio-collared deer were located on lands accessible to hunters and 20% were located on lands with no hunting allowed. During 2011, 84% of radio-collared deer were located on lands accessible to hunters and 16% were located on lands with no hunting allowed.

We recorded 20 adult mortalities; natural causes included starvation ($n = 1$, 4.8%), predation ($n = 3$, 14.4%), unknown winter-related ($n = 6$, 28.8%), and an unknown summer mortality ($n = 1$, 4.87%). Additional causes of mortality included harvest ($n = 6$, 28.6%) and vehicle collisions ($n = 3$, 14.3%). Only model {hunt2010=post2011, rest equal} where survival was similar between hunt 2010 and post-hunt 2011 and differed from remaining seasons that were similar was supported by our data ($w_i = 1.00$);

TABLE 1. Descriptions of candidate set of survival models for adult female White-tailed Deer (*Odocoileus virginianus*) captured in central North Dakota, USA, 2010–2011.

| Model	Description
{hunt2010=post2011, rest equal}	Survival is similar between hunt 2010 and post-hunt 2011 and differs from remaining seasons which are similar
{pre-hunt=post-hunt=hunt}	Survival is similar among seasons
{pre-hunt=post-hunt=hunt, diff year}	Survival is similar among seasons but differs between years
{pre-hunt=post-hunt, hunt}	Survival is similar between pre-hunt and post-hunt seasons which differ from hunt season
{pre-hunt=post-hunt, hunt_diffyear}	Survival is similar between pre-hunt and post-hunt seasons which differ from hunt season which is different between years
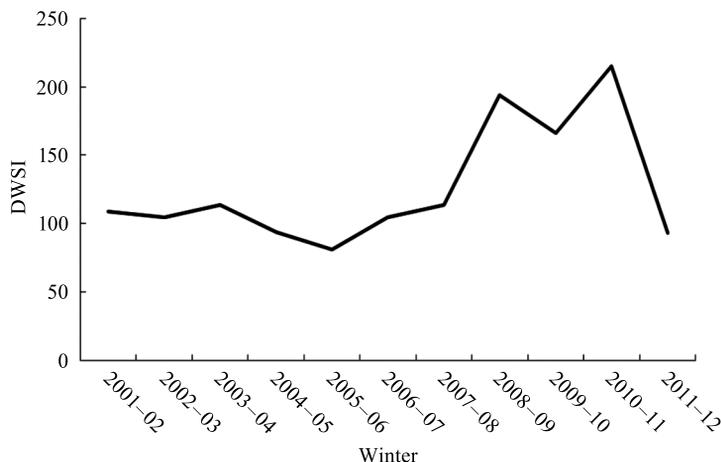
FIGURE 1. Deer winter severity indices (DWSI) for White-tailed Deer (*Odocoileus virginianus*) in central North Dakota, USA.

remaining models were ≥14.86 ΔAIC$_c$ from the top-ranked model (Table 2). Model {hunt2010=post2011, rest equal} indicated that adult survival was similar between hunt 2010 and post-hunt 2011 periods but was lower than other periods. The survival rate for hunt 2010 and post-hunt 2011 was 0.82 (SE 0.04, 95% CI 0.73–0.89) whereas the survival rate for remaining seasons (post-hunt 2010, pre-hunt 2010, pre-hunt 2011, and hunt 2011) was 0.97 (SE 0.01, 95% CI 0.93–0.99).

Discussion

During the very severe winter of 2010–2011 and moderate winter of 2011–2012 (severity based on our analysis), deer in central North Dakota exhibit a mixture of movement strategies consisting of residents, migrators, and late season movers. However, our results indicated that populations in this region were composed largely of residents. Percentage of resident deer (67%: 36 residents in 2010 + 22 residents

in 2011 / 86 total deer) documented during our study was substantially higher than previously reported in the Northern Great Plains (25–46%, Brinkman *et al.* 2005; 22.5%, Burris 2005; 33.3%, Smith 2005; 38%, Grovenburg *et al.* 2009; 50%, Robling 2011), although differences may be related to our methods of classifying deer movement strategies and/or loss of migrators in previous severe winters. Long *et al.* (2005) and Grovenburg *et al.* (2011b) reported deer that inhabited landscapes with limited tree cover were more likely to travel greater distances during migration periods to occupy landscapes with greater forest cover, which provided thermal cover, escape shelter, and food resources. However, microsite characteristics that minimize heat loss (i.e., forested habitat; Moen 1973) may not be critical to deer survival because deer may be able to maintain core temperature via consumption of high quality agricultural feedstuffs, such as waste or unharvested sunflower seeds and corn. Given White-tailed Deer in our study

TABLE 2. Survival model results for adult female White-tailed Deer (*Odocoileus virginianus*) captured in central North Dakota, USA, 2010–2011.

Model	AIC$_c$*	ΔAIC$_c$†	w_i‡	K§	Deviance
{hunt2010=post2011, rest equal}	254.03	0.00	1.00	2	77.76
{pre-hunt=post-hunt=hunt}	268.89	14.86	0.00	1	94.62
{pre-hunt=post-hunt=hunt, diff year}	269.24	15.21	0.00	2	92.97
{pre-hunt=post-hunt, hunt}	269.25	15.22	0.00	2	92.97
{pre-hunt=post-hunt, hunt_diffyear}	269.65	15.62	0.00	3	91.37

*Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).
†Difference in AIC$_c$ relative to minimum AIC.
‡Akaike weight (Burnham and Anderson 2002).
§Number of parameters.

area wintered in agricultural fields, there was likely no switch in browsing physiology from natural forage to agricultural crops. Regardless, White-tailed Deer in the grassland dominated landscapes of central North Dakota likely use unharvested crops instead of forested cover during severe winter weather (Smith *et al*. 2007; Grovenburg *et al*. 2010; Nagy-Reis *et al*. 2019).

We attribute the numerical decrease in resident animals (36 residents in 2010 and 22 residents in 2011) during winter 2011, in part, to the number of animals making late season movements. In our study area, DWSI during 2008–2009, 2009–2010, and 2010–2011 were among the most severe winters recorded for central North Dakota since 1949 and thus, these winters were more severe compared to conditions when other studies on deer movements were conducted in the Northern Great Plains. This variation in winter severity likely affected crop availability between the two winters. For example, by 20 December 2009, 68% of corn was harvested statewide (59% in our study area; USDA 2013). A major snowstorm in late December 2009 continued to delay corn harvest (71% statewide corn harvest by 4 January) and most producers waited until spring to harvest remaining corn (USDA 2013). However, during winter 2010–2011, availability of unharvested crops to deer was minimal; statewide corn harvest was 98% by 22 November 2010 (USDA 2013). All late season movements (*n* = 7) were made by individuals leaving a food source or habitat (e.g., unharvested sunflowers/corn) with no available food remaining or with food that had become inaccessible because of drifting snow. These individuals were likely searching for food as they made late winter movements to a high-energy food source (unharvested corn, residential area). Additionally, 74% of the 86 radio-collared deer we monitored for two winters (43 each year) did not return to the same wintering area within their home ranges. This low degree of site fidelity in home range placement was likely related to forage availability (van Beest *et al*. 2013; Peignier *et al*. 2019) and use of prewinter reconnaissance within the matrix of stable cover habitats (i.e., shelter belts and wetlands).

Between 6 and 20 April 2010 we observed six radio-collared resident deer make non-traditional movements (relatively long-distance movements made during a short duration of time) ranging from 12 to 24 km before returning to their original starting location prior to parturition. These types of movements are referred to as "occasional sallies" (Burt 1943: 351) or exploratory movements (Pépin *et al*. 2008). They may have been movements to locate previously used or known resources that could be acquired during various seasons (e.g., parturition season, winter) for future use. These occasional sallies

might become more prevalent after severe winters such as those that occurred in North Dakota 2009–2011 (Jensen 2009) because of the potential need to travel to and use new food resources. Future research should focus on assessing whether these directed movements are used as a survival strategy during severe winters to better help our understanding of deer survival strategies in the Northern Great Plains.

Migration distances and 95% home ranges that we report were mostly comparable to other studies conducted in the Northern Great Plains (Brinkman *et al*. 2005; Burris 2005; Swanson 2005; Smith *et al*. 2007; Robling 2011). However, our mean migration distances and 95% home ranges were smaller than those reported by Grovenburg *et al*. (2009) in north-central South Dakota. Although many factors can contribute to the documented variation in the Northern Great Plains, we suggest that landscape level habitat characteristics are the most influential factors in spatial variation of migration distances and home ranges (i.e., unharvested agricultural crops; Jensen 1999; Grovenburg *et al*. 2009). Increased demand for biofuel production has caused increased conversion of grassland to cropland (Secchi and Babcock 2007; Searchinger *et al*. 2008; Fargione *et al*. 2009). This increased demand for corn production in the United States resulted in 4.9 million ha of land being converted from grasslands to cropland between 2005 and 2008. Widespread habitat change on this scale could directly affect wildlife populations (Fargione *et al*. 2009). We agree that the rapidly changing landscape (grassland conversion and wetland drainage) within the Northern Great Plains has affected home range size and movement strategies of White-tailed Deer occupying the region (Grovenburg *et al*. 2012). Furthermore, severe winter weather could require White-tailed Deer to engage in an energetically demanding strategy that involves seasonal migration, reconnaissance, and rapid response to resource abundance.

Although we located at least 80% of radio-collared adult female deer on hunter accessible lands, hunter harvest accounted for only ~29% of all mortalities with natural causes (predation, malnutrition, and unknown causes) representing ~52% of total mortalities of deer in our study. Our results support Moratz *et al*. (2018) who reported natural causes (52%) were the leading cause of mortality in the western portion of South Dakota and North Dakota while hunter harvest only accounted for about 19% of all mortalities. However, our results do not support other studies in the Northern Great Plains in which hunting was the primary cause of adult female White-tailed Deer mortality (e.g., 43%, Brinkman *et al*. 2005; 70%, Grovenburg *et al*. 2011a). Regardless, the presence of radio-collars does not seem to deter hunters from harvesting

specific deer (Buderman *et al*. 2014), although there are other reasons why hunter harvest may be limited in the western Dakotas. Limited antlerless tag allocations and short firearm seasons likely influenced hunter harvest in the region for adult females. If so, then the high mortality rate attributed to natural causes may be artificially inflated due to the inability of hunters to effectively harvest female deer in our study area.

Conclusion

Although only associative, our results suggest that adult female White-tailed Deer migration strategies in central North Dakota are likely influenced by the interaction of winter severity and resource availability. We anecdotally observed an increased percentage of resident adults when agricultural crops were unharvested, which further suggests that White-tailed Deer display behavioural plasticity related to winter severity (Giroux *et al*. 2016; Courbin *et al*. 2017). Additionally, mortalities attributed to hunter harvest were low in our study. Harvest management can become conservative during severe winters in anticipation of high natural mortality. However, assuming recreational harvest of White-tailed Deer is compensatory and not additive (Mackie *et al*. 1998), then our results indicate that agencies could maintain or increase harvest opportunity after periods of severe winter weather. Ciuti *et al*. (2015) suggested Pacific decadal oscillations may be useful as predictors of subsequent winter conditions in western North Dakota. Therefore, continual monitoring of migration strategies and survival is needed as landscape level habitat changes continue in the Northern Great Plains (e.g., loss of Conservation Reserve Program, grassland conversion, wetland drainage) and could dramatically influence these life history traits of White-tailed Deer.

Author Contributions

Writing – Original Draft: B.A.S.; Writing – Review & Editing: J.A.J., W.F.J., and E.S.M.; Conceptualization: J.A.J. and W.F.J.; Investigation: B.A.S., J.A.J., and W.F.J.; Methodology: J.A.J. and W.F.J.; Formal Analysis: B.A.S.; Funding Acquisition: W.J.F. and J.A.J.

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Paedomorphic Blotched Tiger Salamander (*Ambystoma mavortium melanostictum*) *in ovo* counts, British Columbia, Canada

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Abstract
Reproductively mature larval morphs, known as paedogens, are a rare occurrence in Blotched Tiger Salamander (*Ambystoma mavortium melanostictum*). The Southern Mountain population of this subspecies, confined to the southern interior of British Columbia, is listed federally as Endangered and has been facing increasing pressures from anthropogenic stressors in both their aquatic and terrestrial landscapes. In 2017, we examined a subset of 36 frozen Blotched Tiger Salamander paedogens collected in September 1985 after rotenone treatment in preparation for a recreational fishery near Oliver, British Columbia. We estimated total *in ovo* numbers in nine gravid individuals to gain insight into paedogen reproductive condition. The number of eggs per individual averaged 227 ± 109 [SD]; range 28–421), with larger dark eggs accounting for 133 ± 69 and smaller pale eggs (possibly follicles or colour may be an artifact of storage) accounting for 94 ± 49. Salamanders were collected in September after the expected egg-laying period for the terrestrial form (early spring); thus, the reproductive stage of the eggs is unclear, but is assumed to be post-breeding and representative of developing eggs and follicles. Canadian data on *in ovo* counts within the body cavity have not been reported for Blotched Tiger Salamander paedogens and our study provides valuable information on the reproductive condition of paedogens. Although terrestrial forms have been observed, the presence of paedogens in the treated wetland has yet to be detected.

Key words: Blotched Tiger Salamander; *Ambystoma mavortium melanostictum*; egg mass; reproduction; life history; neotene; neoteny; paedogenal metamorphosis

Introduction

Paedomorphism is a developmental process found in some urodele amphibians where metamorphosis is delayed, but a sexually mature aquatic adult that resembles its larval form develops and is referred to as a paedogen (Pierce and Smith 1979). Paedomorphism may be a result of complex environmental cues, resources, and site conditions. The occurrence of paedogens in the Southern Mountain population of Blotched Tiger Salamander (*Ambystoma mavortium melanostictum*) in the Similkameen, Okanagan, and Kettle River Valleys of British Columbia is poorly documented and has only been detected in five wetland locations (COSEWIC 2012). Wetlands in the south Okanagan River Valley can have coexisting terrestrial and aquatic breeding forms (S.L.A. pers. obs.; also observed in Mole Salamander [*Ambystoma talpoideum*] by Semlitsch 1985) and the species is generally observed in fishless wetlands (COSEWIC 2012). Historically, wetlands throughout the upper and lower benches of the south Okanagan were most

likely all fishless (J. Mitchell pers. comm. 2008). Salamanders and fish do coexist in a few locations in the south Okanagan, for unknown reasons, although habitat complexity may play a role (Ashpole 2015).

The Southern Mountain population of Blotched Tiger Salamander, a subspecies of Western Tiger Salamander (*Ambystoma mavortium*), is listed federally as Endangered in Canada and restricted to British Columbia (ECCC 2017). Similar to other amphibian species, Blotched Tiger Salamanders experience a variety of anthropogenic pressures, including habitat degradation, fragmentation and isolation, agricultural contaminants, introduced predatory fish species, and increased drought affecting wetland hydrology (ECCC 2017). Because this population is localized at the northern edge of the subspecies' range, its reproductive biology is not completely known and information from southern populations is often presumed (Collins *et al.* 1980; Matsuda *et al.* 2006; IUCN 2015; ECCC 2017). Beyond water body permanence, specific breeding habitat requirements for Blotched Tiger

Salamander paedogens are not clear (COSEWIC 2012). In the terrestrial form, courtship and mating occur after the first heavy rainfall in March or April and cease in May when terrestrial adults return to upland habitats (ECCC 2017). Larvae hatch within three weeks and remain aquatic until early summer (July to August); however, some may overwinter until the following spring (ECCC 2017). The timing of courtship and egg-laying for paedogens is assumed to be similar to that for the terrestrial form.

Disparity of egg mass counts for terrestrial Blotched Tiger Salamander have been reported from American sources, with some research indicating that eggs are singly laid on submerged vegetation (Corkran and Thomas 1996; Collins *et al.* 1980) and others reporting large or variable clusters ranging from 23 eggs (Anderson *et al*. 1971) to 120 eggs (Anderson *et al.* 1971; Corkran and Thomas 1996). The differences in number of eggs per mass laid at one time may be related to the total number of mature eggs present *in ovo* and whether individuals oviposit eggs serially in multiple small clusters or all at once within the season. The only research explicitly examining egg counts from dissected paedogen ovaries reports up to 5670 ± 1021 (SD) per individual (*n* = 13; Rose and Armentout 1976).

Uncertainty about Blotched Tiger Salamander fecundity is especially true for paedomorphic individuals, whose biology and ecology may be different from that of their terrestrial counterparts. Paedomorphs have been observed mostly in warm, shallow, permanent ponds and lake edges where there is little risk of predation by fish or invasive organisms (Collins *et al*. 1980; Whiteman 1994; Corkran and Thomas 1996; Anderson and Whiteman 2015). The reproductively mature larval form has been observed to occur in other *Ambystoma* salamanders as a result of environmental and interspecific species relations; paedomorphism is theorized to increase fitness under specific environmental conditions (e.g., high resource availability, optimal aquatic habitat; Semlitsch and Wilbur 1989; Denoël *et al*. 2005; Anderson and Whiteman 2015).

Here we record *in ovo* counts from the dissected ovaries of paedogens from the Southern Mountain population of Blotched Tiger Salamanders recovered from a permanent wetland after a rotenone treatment to eradicate Pumpkinseed Sunfish (*Lepomis gibbosus*), Rainbow Trout (*Oncorhynchus mykiss*), and Small-mouth Bass (*Micropterus dolomieu*) in preparation for a trout fishery.

Methods

Dead adult Blotched Tiger Salamanders were collected after a rotenone treatment in September 1986 near Oliver, British Columbia (49.1823°N, 119.5504°W; Ministry of Environment 1986). In total, 176 salamanders were collected (19 unknown sex presumed juvenile, 92 females, 65 males). Although the species was validated and notes on sex based on gross morphology were made by experienced local herpetologists, it is unclear from the records if all collected individuals were paedogens. A subsample of 36 frozen (–18°C) paedogens was retained and re-examined in 2014, necropsied, measured, stomach contents macroscopically inspected, and sexed using gross morphology (presence of oviducts and/or eggs or testis). It is not clear why this particular subset of 36 specimens was retained and the subset may represent a biased sampling of individuals from the population. Whole sunfish were detected in the oral cavity or stomach contents of seven salamanders. A subsample of 11 females was subsequently placed in individual specimen jars filled with ethanol and stored. The subsample was selected based on well-preserved intact specimens; decayed or damaged individuals were discarded. In 2017, eggs were removed from each individual and counted using a stereomicroscope (16× magnification; Zeiss Stemi, Model 3919021628, Jena, Germany). To ensure accuracy during egg counts, S.L.A. and M.R.N. conducted independent (blind) counts of each mass and recorded total number of eggs, eggs that appeared notably smaller or paler, and larger dark eggs (Figure 1).

Results

The 176 adult specimens collected were female biased, with a ratio of 1.4 females to every male, assuming sexing was accurate. From the more closely

FIGURE 1. Eggs of a paedomorphic Blotched Tiger Salamander (*Ambystoma mavortium melanostictum*) from near Oliver, British Columbia, Canada, observed through a stereomicroscope (16×). Eggs were either smaller, pale, immature (white circle) or larger, dark, mature. Photo: S. Ashpole.

examined subsample of 36 specimens, 17 were of unknown sex (presumed immature; mean total length [TL] ± SD 12.0 ± 1.0 cm; range 9.8–13.6 cm), five were male (TL 14.3 ± 1.6 cm; range 13.8–17.5 cm), and three were non-gravid females (TL 17.0 ± 0.5 cm; range 16.3–17.3 cm). The remaining 11 specimens were gravid females and the largest of the subsample (TL 18.0 ± 1.7 cm; range 16.2–22.0 cm). Two of the latter were omitted from egg counts because of decomposed egg tissue.

Egg masses in each of the nine gravid females were found to consist of both smaller (3–6 mm) and larger eggs (7–11 mm), with large eggs 1.5 times bigger than small eggs and darker brown to black in colouration. Immature eggs were smaller, much lighter in colour, and less numerous than mature eggs. The eggs were contained in translucent gelatinous sacs located bilaterally within the individual, ventral to the kidney structures. Number of eggs in each female varied considerably, from 28 to 421 (average 227 ± 109), with larger dark eggs accounting for 133 ± 69 and smaller pale immature-looking eggs accounting for 94 ± 49 per individual. The total number of eggs per female was positively correlated with total body length (r = 0.98; Figure 2). Inter-observer variability was low for total number of eggs (± 4 eggs), but slightly higher for counts of larger dark eggs and smaller pale eggs (± 18 eggs).

Discussion

The number of eggs in an individual paedomorphic Blotched Tiger Salamander (28–421) was considerably smaller than estimates provided in the recovery strategy for the terrestrial form of this species (5000 eggs/mass based on Rose and Armentrout 1976; ECCC 2017). The difference, which was at least one order of magnitude, has substantial conservation implications for protection and management of the species. Our findings are comparable to those of Collins *et al.* (1980), who reported terrestrial forms with 23–110 eggs/mass, although our counts represent total number of eggs in the body cavity versus ovideposited eggs. It is not clear how eggs are deposited by paedogens and whether deposition occurs in a single event or as several clusters over time. Similarly, the developmental cycle of eggs in our species is not documented, but presumed to be similar to the terrestrial form because of the timing of environmental conditions. Previous studies have reported location and distribution of terrestrial *A. mavortium* egg-laying sites within their habitat (Anderson *et al.* 1971; Sever and Dineen 1977; Collins *et al.* 1980; Corkran and Thomas 1996; Ministry of Environment and Climate Change Strategy 2014), but information on paedogens remain undocumented. Egg-laying characteristics may be particularly challenging if eggs of the terrestrial form are indistinguishable from those of the aquatic form.

Similarly, it is not clear whether the reproductive cycle or ecology of Blotched Tiger Salamander paedogens in the southern interior of British Columbia are similar to those of other populations of this subspecies in British Columbia or other morphs, throughout the subspecies' range. Rose and Armentout (1976) report discontinuities of gene flow in western subspecies of tiger salamanders, leading to significantly
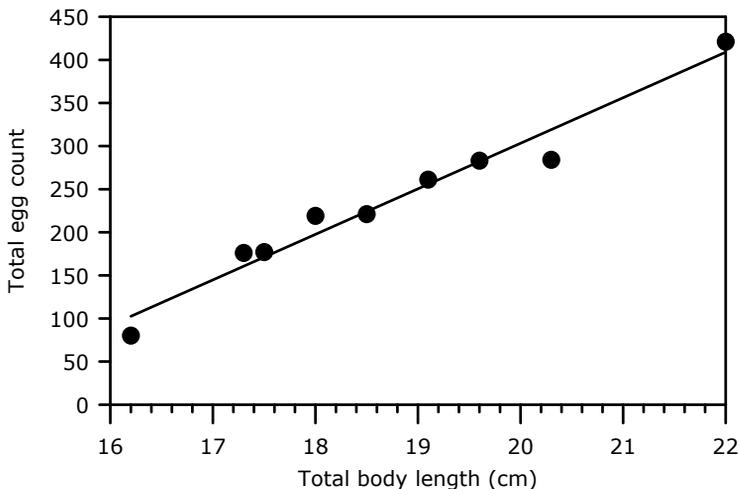
FIGURE 2. Positive correlation between total body length of nine gravid female paedomorphic Blotched Tiger Salamanders (*Ambystoma mavortium melanostictum*) from near Oliver, British Columbia, with total egg count (Pearson product-moment correlation coefficient, r = 0.98).

variable metamorphic rates, size limits, and some physiological parameters. Female paedogens in our population ranged from 17.0 to 22.0 cm TL, whereas the largest females reported by Rose and Armentout (1976) from New Mexico were smaller at 14.3 cm (range 13.9–14.7 cm). California Tiger Salamander (*Ambystoma californiense*) males averaged 20.1 cm and females averaged 16.8 cm in TL, with sex ratios varying from 0.8:1 (1992) to 8.1:1 (1993; Loredo and Van Vuren 1996). The variability suggests that information gleaned from our study should remain within the south Okanagan context.

As paedogens occur in permanent aquatic habitat, it is also possible that the conversion of wetlands in the southern interior to ephemeral, human-made ponds (Lea 2008) may lead to smaller populations of the paedogenic form because of lack of suitable habitat throughout the area. More investigation into the reproductive biology and behaviour of Blotched Tiger Salamander, in all forms, is required to accurately elucidate the reproductive potential of this species and inform recovery efforts and conservation of wetlands. For this particular site, terrestrial salamanders have been observed, but paedogens have not been detected since the rotenone treatment. Confirmation of the continued presence or re-establishment of tiger salamander paedogens will require more intensive surveying. Further examination of the persistent effects of rotenone applications on these important permanent wetland habitats is critical for conservation of amphibian species as recreational fish management continues. Finally, we are still uncertain how such a large number of paedomorphic salamanders survived and were subsequently salvaged from a wetland in the presence of introduced predatory fish. Sunfish and bass species are known predators of amphibian larvae (Riley *et al.* 2003; Preston *et al.* 2012) and are thought to have a severe impact on amphibian larvae. It is often assumed that paedomorphic salamanders are excluded from sites with predatory fish (Sprules 1974; COSEWIC 2012).

Author Contributions

Writing – Original Draft: M.R.N.; Writing – Review & Editing: S.L.A.; Conceptualization: S.L.A.; Investigation: M.R.N. and S.L.A.; Methodology: S.L.A.; Formal Analysis: M.R.N. and S.L.A.; Funding Acquisition: S.L.A.

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Hiding in plain sight: combining field-naturalist observations and herbarium records to reveal phenological change

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Abstract
As the climate warms, northern ecosystems are experiencing warmer winters and seasonal climatic shifts. Vascular plants are expected to respond to climate change by adjusting flowering or seeding periods. To determine how a native mixed-wood boreal floral assemblage has responded to warming temperatures over the 20th century, we collated historical observations made by field-naturalists as well as voucher data from the Thunder Bay region of Ontario, Canada. Combining these datasets, we performed regression analyses on 11 species of spring-flowering vascular plants to evaluate temporal trends and used spring cumulative growing degree day ($sGDD_0$) to determine the influence of climate on flowering times. Four species showed consistent positive temporal trends (i.e., flowered later with time), while four species (three of which also demonstrated temporal trends) showed negative trends with $sGDD_0$ (i.e., flowered earlier with an increased number of degree days above 0°C). The unexpected observation of later flowering times but predicted observation of earlier blooming with increased $sGDD_0$ indicates that the inclusion of climate metrics may be necessary to determine the response of native vascular plants to the onset of changes in their environment. These observations were not statistically significant when field-naturalist or herbarium voucher data were analyzed separately, possibly due to low statistical power. Combining data from both sources, however, revealed common responses to climate warming among species within an ecoregion.

Key words: Climate change; phenology; Ontario; boreal mixed woods; angiosperms

Introduction

Anthropogenic activity is unequivocally altering global climate, with significant and observable effects on ecosystems (Hoegh-Guldberg and Bruno 2010; Woodward *et al*. 2010; Burrell *et al*. 2020). The earth's climate has increased 0.74°C on average over the last 100 years, and the Intergovernmental Panel on Climate Change (IPCC) projects a continued rise of 0.2°C in each following decade (Trenberth *et al*. 2007; IPCC 2018). Rising global temperatures have many environmental side effects, among them the melting of polar ice caps, increased drought, and unpredictable extremes for regular climatic events such as El Niño and La Niña (Fischer and Knutti 2015; Stott 2016; Teng *et al*. 2016; Jia *et al*. 2019). These abiotic climatic changes affect organisms living in these environments in ways that are acute, long-term, or both (Rodenhouse *et al*. 2009; Last *et al*. 2011; Pecl *et al*. 2017). Perhaps the most likely to be affected, especially in northern latitudes, are organisms reliant on temperature-specific cues to time their lifecycles.

Climate-change-related temperature increases are most pronounced in temperate, Antarctic, and Arctic regions, with the most dramatic changes expressed as increases in mean winter temperature and a contraction of the length of winter (e.g., Beaumont *et al*. 2011; Guzzo *et al*. 2017). These climatic changes have the potential to alter a variety of seasonally dependent phenotypes in plants, animals, and other organisms, such as timing of migration, reproduction, food acquisition, and frequency of reproductive bouts (Both *et al*. 2010; Bussière *et al*. 2015; Goulson *et al*. 2015; Green 2017; Tao *et al*. 2018). Decoupling or mis-timing of these cues can result in a variety of deleterious

outcomes including reproductive failure (Williams *et al*. 2014; Tao *et al*. 2018), changes in energetic coupling (Guzzo *et al*. 2017), or mismatches in responses of different trophic levels to different environmental cues leading to reduced energy transfer and decreased survival (e.g., Winder and Schindler 2004). An adaptive response to these outcomes is to migrate to cooler latitudes, which may have an effect on the pre-existing flora and fauna of that region (Schmidt *et al*. 2012). Species that are reliant on environmental cues are thus dependent on their ability to adapt to new climatic norms, respond by phenotypic plasticity, or their ability to migrate to new habitats to survive.

Phenology, the study of the seasonal lifecycle of organisms, will play a role in determining how these organisms adapt to a warming environment. Phenological cues can either be independent of climate (e.g., number of daylight hours) or climate dependent (e.g., soil temperature, type or amount of precipitation). While equatorial ecosystems often rely on predictable changes in the moisture regime with largely stable temperatures (Borchert 1996; Marques *et al*. 2004), temperate organisms are often reliant on the onset of spring to initiate their lifecycles, signalled by snowmelt, increased daylight hours, and warmer temperatures. The ability to capitalize on these conditions is often critical to an organism's ability to survive and produce offspring.

In plants, climatic challenges related to phenology may be greater than in animals (Cleland *et al*. 2007). While shifts in elevational or latitudinal distributions are predicted for both animals and plants to maintain an optimal thermal environment, the reliance of vascular plants on seeding success for this distributional shift (rather than active individual movement) is an intrinsically slower process; extirpations of local populations have been observed in several species as individual plant populations fail to adapt to new climatic conditions (Wiens 2016). Previous studies of vascular plant phenology have shown that consecutive warmer springs result in earlier flowering (Fitter *et al*. 1995; Miller-Rushing and Primack 2008; Beaubien and Hamann 2011a; Panchen *et al*. 2012), but patterns are not consistent across taxa, variably showing earlier, delayed, or neutral responses to increasingly warm springs (Cook *et al*. 2012; Ziello *et al*., 2012; Hart *et al*. 2014; Hufft *et al*. 2018; Panchen and Gorelick 2017). Of the temperate vascular plants previously studied, those that bloom in early spring often show an increased sensitivity to mild winters and early-arriving springs, blooming days earlier than their late spring or summer counterparts (Lavoie and Lachance 2006; Miller-Rushing and Primack 2008; Willis *et al*. 2010; Ellwood *et al*. 2013).

To determine if and how assemblages of plants are responding to climate change, long-term datasets are critical. Museums hold a wealth of information that can be used to address phenology; vouchers of botanical specimens provide a record of location, range, and flowering stage. Collected over many years, they also provide a valuable account of plant phenology and occurrence through both time and space. However, herbarium collections can show biases, including curator bias towards particular taxa or a tendency for vouchers to be collected from only accessible locations (Willis *et al*. 2017). In spite of these biases, herbarium vouchers often form the basis of historical phenological studies in plants (Everill *et al*. 2014; Panchen *et al*. 2014, 2019; Park and Schwartz 2015; Riera *et al*. 2015; Daru *et al*. 2018; Park *et al*. 2019), which can also be coupled with short-term citizen science observations or field studies (Morisette *et al*. 2009; Spellman and Mulder 2016). Along these lines, amateur field-naturalist (hereafter simply field-naturalist) records can provide another source of information that remains largely unmined for potentially informative phenological data (Miller-Rushing *et al*. 2012).

Field-naturalist observations have been made for centuries, often with a goal of determining timing and location of agricultural harvest, but also with an interest in observing the natural world. Perhaps the most famous North American example is Henry David Thoreau's recording of natural events in and around Walden Pond, in Concord, Massachusetts (Miller-Rushing and Primack 2008). Detailed individual accounts like Thoreau's are the exception, but in the 20th century we see the rise of organized groups of field-naturalists who often recorded local natural events over time. This practice continues in the form of citizen science projects including the USA Phenology Network (https://www.usanpn.org/usa-national-phenology-network), and the Canada PlantWatch program (https://www.naturewatch.ca/plantwatch/).

Northwestern Ontario, located on edge of the boreal Canadian Shield, presents a unique opportunity to determine how phenology is changing in a previously understudied part of Canada, with records of vascular plant phenology available through written records kept by the Thunder Bay Field Naturalists (TBFN; https://tbfn.net), as well as in the holdings of the Claude Garton Herbarium (LKHD) at Lakehead University. In Canada, studies that use historical or herbarium data to examine changes in phenology are growing in number. Several have been conducted in the last 30 years that have examined climatic effects on seasonality of herbaceous plants in Quebec, Alberta, and regions of the high Arctic (Lavoie and Lachance 2006; Houle 2007; Beaubien and Hamann 2011a; Kharouba *et al*. 2014; Panchen and Gorelick

2017; Prevéy *et al.* 2017; Park *et al.* 2019). To date, no study of this nature has been conducted in north-western Ontario and we believe this to be the first study to use long-term phenological records kept by the TBFN.

The goal of our study was to determine climate-related phenological changes in early-flowering vas-cular plants from several common plant families in northwestern Ontario. As no work of this nature has been done in the region, we chose a variety of angio-sperm taxa well represented in both herbarium and field-naturalist datasets from different families. We hypothesize that the earliest blooming species will be the most sensitive to changes in climate and will flower significantly earlier through time.

Methods

Study area

Northwestern Ontario is located on the Canadian Shield and is bounded by the U.S. Minnesota border and the Great Lakes to the south, Hudson's Bay to the north, Manitoba to the west, and Timmins, Ontario, to the east (Figure 1). The Thunder Bay region, where many of the collections or observations included here were made, encompasses ~103 722 km² and is composed of several large tracts of Canadian Crown land that transitions from southern mixed-wood for-ests into boreal forest. These forests are dominated by birch (*Betula* spp.), poplar (*Populus* spp.), spruce (*Picea* spp.), pine (*Pinus* spp.), and various shrubs (alder, willow [*Salix*]). The understorey is largely her-baceous, with 119 families of vascular plants present (TBFN 2015).

Climate data

Historical daily average temperatures were ob-tained from Environment and Climate Change Can-ada (ECCC; Government of Canada 2019) from five weather stations within a 25 km radius of the city of Thunder Bay (Figure 1), the area in which 70% of the herbarium vouchers were collected (*n* = 271/399) and 100% of the naturalist observations were made (see below). Recorded temperatures in this area span al-most 140 years, from 1878 to 2017. Where multiple
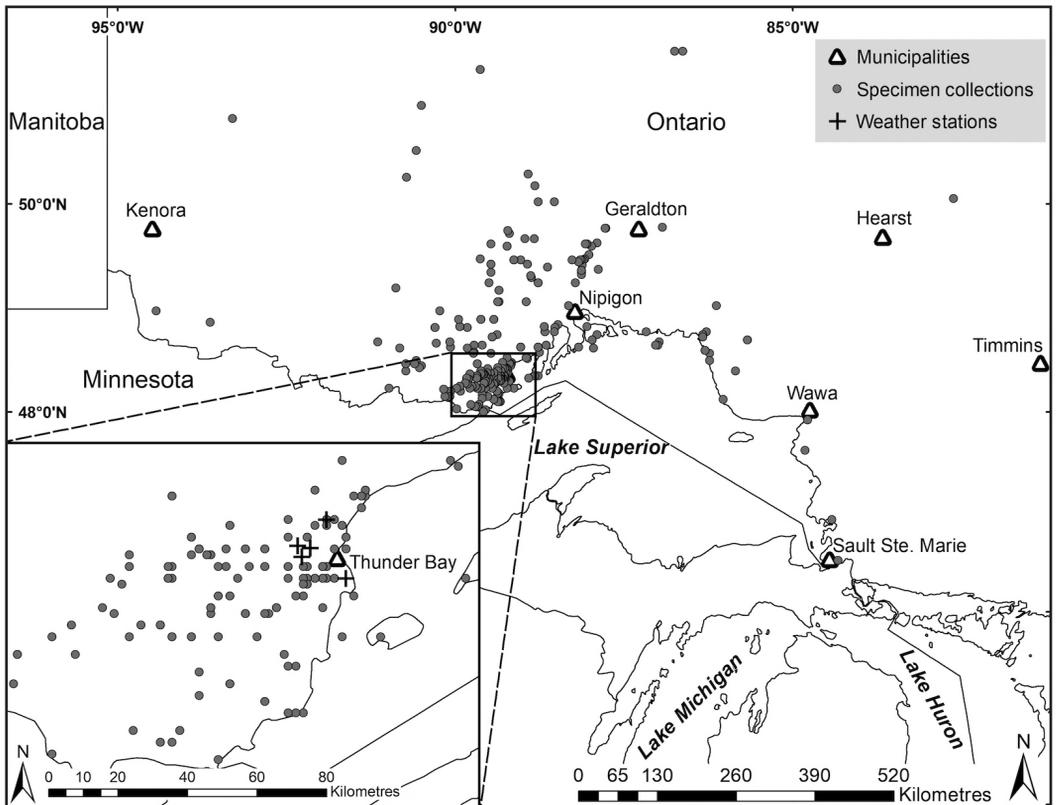
FIGURE 1. Map showing Thunder Bay region with collection localities of included vouchers. Of the 399 vouchers from the Claude Garton Herbarium (LKHD) included, 29 lacked GPS co-ordinates and are not shown here. Weather stations are denoted with a cross.

daily temperatures from several stations were recorded, we used the average value of all stations with useable data (i.e., those not flagged as erroneous by ECCC). Although the first and last phenological observations in our dataset occurred in 1932 and 2006, respectively, we included all available climatic data in this region to attempt to capture possible changes in the long-term climate record. Mean annual temperature was estimated as the 365-day average of daily means.

All five stations were used to generate a complete dataset with daily average temperatures and very few stations had periods of overlap with regard to data availability. As most observations were concentrated in the Thunder Bay region, we used mean daily temperatures from this area as indicative of climate in the region generally. Given the broad temporal (e.g., annual averages) scale of our analysis, minor regional deviations in microclimate across our study region were assumed to be negligible. To validate this assumption, we compared mean annual temperatures between our dataset and one at the IISD Experimental Lakes Area, 600 km west of Thunder Bay (date range of comparison 1970 to 2013). The relationship between estimates from both stations (forced through the origin) was not significantly different from 1:1 (t_{43} = 1.43, P = 0.07), suggesting that the Thunder Bay weather stations were representative of the region generally.

Because many early spring-flowering plants are thought to rely on temperature cues to begin their phenological cycle, we use cumulative growing degree days (GDD) greater than 0°C over the spring period ($sGDD_0$ hereafter). Cumulative GDD are used to measure the ambient air temperature above a threshold temperature from germination or reactivation in perennial species to a given life stage, here peak flowering of spring plants. Although GDD is a measure of ambient air temperature, it has been used as a metric of phenology and growth patterns to determine the importance of climate in dictating the life history of many taxa, including fishes, insects, and plants (Neuheimer and Taggart 2007; Mulder *et al*. 2017).

As minimum growth temperatures for our species are not known, we set our base temperature at 0°C, the minimum temperature at which most C3 plants are able to grow (Dürr *et al*. 2015). A lower temperature threshold of 0°C has been used elsewhere in plant growth investigations that include early flowering plants (Abrami 1972). Further, it has been demonstrated that root development in cold-adapted species (including species of Ranunculaceae and Asteraceae, well represented in our study; Table 1) begins at between 0 and 1°C (Nagelmüller *et al*. 2017). As all the plants under investigation here are early ephemerals adapted to begin growth in cold environments shortly after snow melt, the common reference point of 0°C was assumed to be suitable across all species, and also provides comparable estimates across species.

We defined "spring" as the period from 1 February to 31 May. These dates were chosen because (a) few non-zero GDD values were observed between 1 January to 1 February in the study region over the period investigated (indeed, including January had no impact on our $sGDD_0$ estimates; data not shown), (b) this span of time included the typical flowering period for all species studied, and (c) the inclusion of months after the known blooming period has been shown to weaken the statistical relationship between temperature and flowering timing in other phenological

TABLE 1. Species used in climate trend evaluations, Thunder Bay Region, Ontario, Canada. Number of observations from Thunder Bay Field Naturalists (TBFN) newsletters and vouchers at the Claude Garton Herbarium (LKHD) are indicated.

Family	Species	Common name	Range of years evaluated	TBFN (*n*)	LKHD (*n*)
Ranunculaceae	*Anemone quinquefolia* L.	Wood Anemone	1933–1983	19	85
Ranunculaceae	*Caltha palustris* L.	Yellow Marsh Marigold	1948–1992	19	50
Montiaceae	*Claytonia caroliniana* Michaux	Carolina Spring Beauty	1937–1992	17	109
Ericaceae	*Epigaea repens* L.	Trailing Arbutus	1954–1994	14	63
Rosaceae	*Fragaria vesca* L.	Wild Strawberry	1949–1991	17	43
Ranunculaceae	*Hepatica americana* (de Candolle) Ker Gawler	Round-lobed Hepatica	1949–1992	22	50
Asteraceae	*Petasites frigidus* (L.) Fries	Coltsfoot	1933–1992†	23	94
Salicaceae	*Salix discolor* Muhlenberg	Pussy Willow	1949–1981	15	171
Papaveraceae	*Sanguinaria canadensis* L.	Bloodroot	1932–1994	29	66
Violaceae	*Viola pubescens* Aiton	Yellow Violet	1950–2003	12	72
Violaceae	*Viola selkirkii* Pursh ex Goldie*	Selkirk's violet	1933–2003	0	155

*LKHD data only; only three TBFN observations available, none noted as "in bloom".
†2017 outlier removed.

studies of temperate vascular plants (Mulder *et al.* 2017). To calculate $sGDD_0$, mean daily temperatures greater than 0°C were summed from 1 February to 31 May. We additionally estimated GDD_0 to bloom, where the cumulative GDD_0 was estimated for each year that blooms were observed for each species.

Phenological data

We focussed our study on 11 species of perennial angiosperms from eight families found in northwestern Ontario (Table 1). These species were chosen as they represented the plants with the greatest number of records between TBFN and herbarium datasets, and also showed the earliest flowering patterns in the region. It should be noted that herbarium collections and observations do not cover the entire defined Thunder Bay region; most of these data originate from the southern townships east and west the city. Of the 11 included species, all are herbaceous with the exception of Pussy Willow (*Salix discolor* Muhlenberg), which is woody and usually the first to flower locally.

Herbarium vouchers were used to score flowering through time in the 11 chosen species. When a voucher had more than one specimen, these were scored individually and treated as individual observations in the dataset. All herbarium vouchers studied (*n* = 399; Table S1) are housed in LKHD. While most specimens had an associated latitude and longitude, a small number of older vouchers did not (Table S1). We identified those associated localities that fell within the Thunder Bay region using maps. If a locality was outside of this region or could not be identified due to vague locality description (*n* = 29), it was not included. The pressing quality of vouchers can vary, so only specimens with clear stages of flowering were scored and included in the herbarium dataset. Collection dates for focal plant species began in 1932 and end in 2006.

All field-naturalist observations (*n* = 190; Table S1) were made by members of the TBFN. This organization has kept phenological records as part of their membership newsletters from 1947 to present; newsletters are digitized and publicly available on their website (https://tbfn.net/). Three to five newsletters have been published each year, with each issue containing a detailed section on member-reported local phenology of plants, birds, and other wildlife. For angiosperms, the recorded data were most often first flowering of the year, alongside notable locations of rare species; occasionally senescence was noted as well. For our dataset, we included only spring observations in which the state of the plant was explicitly stated (e.g., "in flower"). When a notation of phenological state included flowering, it was assumed that peak flowering was being observed. Recorded sightings by the TBFN are focussed primarily in the city of Thunder Bay (formerly two separate towns, Fort William and Port Arthur) and the nearby townships of Dorion, Neebing, and Oliver-Paipoonge (Table S1).

Collection of vascular plants by herbarium staff occurred from 1932 until 1994, and on a yearly basis until the 1970s, when collections began to decline. In all, herbarium records encompass ~60 years of data. Likewise, the TBFN newsletters contain phenological records of local vascular plant species from 1948 until the 1980s when the records began to be less regularly reported in the newsletters. Each of the species included in the study was represented within both datasets except Selkirk's Violet (*Viola selkirki* Pursh ex Goldie), which was found in LKHD records only.

Phenological coding

A variety of approaches have been used to determine the stage of phenology in flowering plants, especially with respect to herbarium vouchers (Everill *et al.* 2014; Rawal *et al.* 2015; Willis *et al.* 2017; Hufft *et al.* 2018). We numerically coded our plants based on an eight-stage phenological scale, starting with first leaf out (1) and ending with fall senescence (8; Table 2), adapting and expanding on coding stages proposed by Haggerty and Mazer (2008). Collection dates were

Table 2. Coded stages of phenology used to determine flowering stage used in the study, Thunder Bay region, Ontario, Canada.

Stage of phenology	Description
1	Leaf buds present but not opened
2	First leaf is fully expanded
3	Entire plant is leaf out with only buds present
4	First flower is fully open
5	Peak flowering is occurring (largest floral display, >50% of flowers on individual plants are open)
6	Last flower
7	Fruit maturity and/or seed dispersal
8	Leaves are withered and discoloured (senescence)
X	Status cannot be determined from voucher or observation

converted to numerical day of year to facilitate analysis of phenological trends across years. Because our main interest was determining if the timing of blooms in early-flowering species was responding to variation in spring conditions, and to provide comparable data between datasets, we focussed on peak flowering (stage 5), the period during which 50% or more of the present flowers are open simultaneously on a given individual plant. Peak flowering has been used to measure phenological changes in response to climate change and is thought to be a more accurate predictor of population response time than first flowering events as it represents a measure of central tendency of the bloom period, rather than the extreme of first flowering date (Miller-Rushing and Primack 2008; CaraDonna *et al.* 2014; Zhang *et al.* 2018). Finally, while other stages of phenology are important and classically understudied (e.g., autumn; see Gallinat *et al.* 2015), most of the LKHD collections and TBFN observation included were gathered in spring or summer, not allowing the inclusion of any other developmental stage of the plants to be considered here.

On herbarium vouchers with multiple individual plants included on a single voucher, plants were each coded individually, with the assumption that they represented collections of individuals from the same population. If the entire record for the plant in a given year was a single voucher with single or multiple plants in bloom, this was used to estimate peak flowering date. We calculated a weighted average of the day of year for peak bloom only if multiple vouchers occurred in the same year, using the proportion of individuals at peak flowering on the voucher as our weighting term. Weighted means were calculated using the *summarize* function in R (version 3.6.2, R Core Team 2019) package "dplyr" (Wickham 2011).

Bloom records from TBFN newsletters (Table S1) were entered by hand from newsletters. Each botanical record made by the TBFN was assigned a stage of flowering, if noted, on the eight-stage scale. The phenological stage code assigned to each year was then assigned a binary code; 1 for peak flowering and 0 for any other stage. If no observation of phenological stage was included, the record was coded with an "X" to denote stage unknown. Similar to herbarium specimen data, dates of recorded sightings were converted into numerical day of year.

Because Wild Strawberry (*Fragaria vesca* L.) blooms multiple times through the season, we limited the reported bloom dates to those occurring prior to 20 July (day of year 200), given that we were primarily interested in the patterns of spring blooming of plants. For both LKHD and TBFN datasets in the Thunder Bay region, the number of observations for each species included varied between datasets, ranging from three (Selkirk's Violet, TBFN) to 171 (Pussy Willow, LKHD; Table 3).

Statistical analyses

Analyses were conducted using R (version 3.6.2, R Core Team 2019). Mean dates of flowering and GDD_0 for each species were estimated (Table 3). Temporal trends in climate data (mean annual air temperature, $sGDD_0$) were evaluated using linear regression. To determine relationships between day of year of peak bloom and year of collection, a simple

TABLE 3. Estimated mean day of bloom and mean growing degree days (GDD) greater than 0°C (units of degree days) to bloom across all observations in the Thunder Bay region, Ontario, Canada. GDD_0 to bloom estimated as the sum of daily temperatures above zero until observed bloom date in a given year; mean across all years with reported bloom dates are presented. n = sample size are shown for both the Thunder Bay Field Naturalist (TBFN) and Claude Garton Herbarium (LKHD) datasets.

Species	Mean day of bloom	SE	Mean GDD_0 to bloom	SE	Total peak flowering	
					TBFN (n)	LKHD (n)
Wood Anemone	144 (24 May)	± 3.2	288	± 28	11	22
Yellow Marsh Marigold	150 (30 May)	± 3.3	376	± 39	18	28
Carolina Spring Beauty	136 (16 May)	± 2.4	129	± 17	12	23
Trailing Arbutus	139 (19 May)	± 3.5	249	± 18	11	18
Wild Strawberry	148 (28 May)	± 5.8	410	± 66	6	16
Round-lobed Hepatica	135 (15 May)	± 2.5	215	± 22	15	32
Coltsfoot	135 (15 May)	± 2.7	238	± 23	18	34
Pussy Willow	117 (27 Apr)	± 8.1	135	± 26	8	11
Bloodroot	133 (13 May)	± 2.0	205	± 20	14	37
Downy Yellow Violet	151 (31 May)	± 2.9	380	± 32	14	20
Selkirk's Violet*	148 (28 May)	± 2.5	338	± 31	0	14

*Only herbarium records.

regression was applied to each species using the peak bloom time estimated for each year. When simple linear regression was applied to only LKHD and TBFN datasets separately, they tended to have weak or non-existent trends for all species; therefore, only the combined dataset trends are reported here. The combined datasets were examined to determine the relationship between peak bloom and $sGDD_0$ using linear regression. Assumptions of homogeneous and normally distributed residuals were evaluated visually and data transformations were applied to peak bloom time when necessary to satisfy these assumptions (Table 3). Relationships were reported as significant for all P below a critical alpha of 0.1. We chose this more liberal threshold to help emphasize commonalities of temporal trends among species apparent in the data, which, given their consistency in both direction and magnitude across several species (see Results), we believe are unlikely to result from spurious associations. Where significant patterns were observed, the mean predicted change over the period investigated for each species was calculated. For each species, between one to five years had observations from both datasets. We used these data with observations from both datasets to conduct a paired *t*-test across all species to determine how closely the TBFN and LKHD records compared to one another.

Results

Mean annual air temperature increased significantly from 1878 to 2017 ($F_{1,135}$= 14.4, P = 0.0002, r^2 = 0.1), increasing by 1.04°C over the nearly 140-year period on average (Figure 2a; see Table S2 for raw data). Similarly, we also observed an increase in $sGDD_0$ with time ($F_{1,138}$ = 15.8, P = 0.0001, r^2 = 0.1), increasing by 86.8 degree days on average over the nearly 140-year period investigated (Figure 2b). There was a significant positive relationship between $sGDD_0$ and mean annual air temperature ($F_{1,135}$ = 90.9, P < 0.0001, r^2 = 0.4; Figure 2c).

The 11 species included in this study were all confirmed to be early blooming, with mean peak bloom dates ranging between 27 April for Pussy Willow and 31 May for Downy Yellow Violet (*Viola pubescens* Aiton), and mean $sGDD_0$ ranging between 129 (Carolina Spring Beauty [*Claytonia caroliniana* Michaux]) and 410 degree days (Wild Strawberry; Table 3). One hundred fifty-nine vouchers (of 399) showed 359 individual specimens during their peak flowering period (stage 5); 116 of 190 TBFN observations were recorded as "in bloom".

In four of the 11 species evaluated (Table 4, Figure 3), we observed a substantial lag in peak bloom over time. This trend was observed in Wood Anemone (*Anemone quinquefolia* L.: 38-day delay on
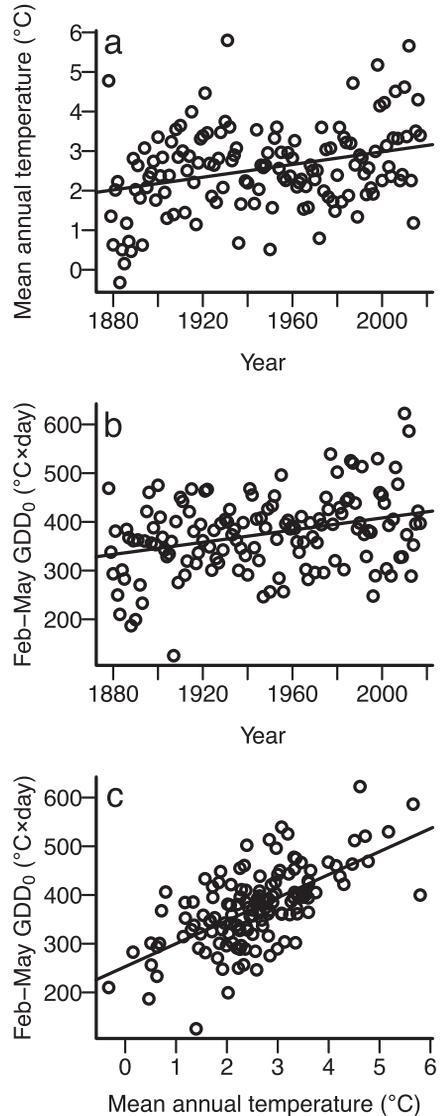
Figure 2. Changes in climate in the Thunder Bay region over the past ~130 years. a. Mean annual temperature in the region has increased ($F_{1,135}$= 14.4, P = 0.0002, r^2 = 0.1), with increasing variability since ca. 1960. b. Growing degree days >0°C between February and May (describing thermal conditions in the spring in the region) have also increased during the same period ($F_{1,138}$ = 15.8, P = 0.0001, r^2 = 0.1). c. Spring cumulative growing degree day ($SGDD_0$) is positively related to mean annual temperature in the region ($F_{1,135}$ = 90.9, P < 0.0001, r^2 = 0.4).

average from 1952 to 1983), Bloodroot (*Sanguinaria canadensis* L.: 19-day delay from 1932 to 1994), Carolina Spring Beauty (29-day delay from 1937 to 1992), and Wild Strawberry (53-day delay from 1949 to 1992). Wood Anemone showed a significant

TABLE 4. Statistical results for evaluations of trends over time and with spring GDD_0 (growing degree days from February to May greater than 0°C), Thunder Bay region, Ontario, Canada. Statistically significant relationships ($P < 0.1$) are in bold.

Species	Trend with year		Trend with spring GDD >0°C	
	Test statistic	P	Test statistic	P
Wood Anemone*	**$F_{1,15} = 20.40$**	**<0.01**	**$F_{1,20} = 3.54$**	**0.08**
Yellow Marsh Marigold	$F_{1,26} = 0.08$	0.77	$F_{1,26} = 0.00$	0.95
Carolina Spring Beauty	**$F_{1,21} = 8.80$**	**0.01**	**$F_{1,21} = 5.08$**	**0.04**
Trailing Arbutus	$F_{1,16} = 0.11$	0.74	$F_{1,16} = 0.14$	0.71
Wild Strawberry	**$F_{1,14} = 3.30$**	**0.09†**	**$F_{1,14} = 3.25$**	**0.09**
Round-lobed Hepatica	$F_{1,30} = 0.10$	0.76	**$F_{1,30} = 7.44$**	**0.01**
Coltsfoot	$F_{1,32} = 0.17$	0.69	$F_{1,32} = 0.56$	0.46
Pussy Willow	$F_{1,9} = 1.21$	0.30	$F_{1,9} = 0.13$	0.73
Bloodroot	**$F_{1,35} = 5.34$**	**0.03**	$F_{1,35} = 0.33$	0.57
Downy Yellow Violet	$F_{1,18} = 1.02$	0.33	$F_{1,18} = 0.59$	0.45
Selkirk's Violet	$F_{1,12} = 0.02$	0.88	$F_{1,12} = 0.13$	0.72

*Trend excludes data earlier than 1950.
†Results for log-transformed data.
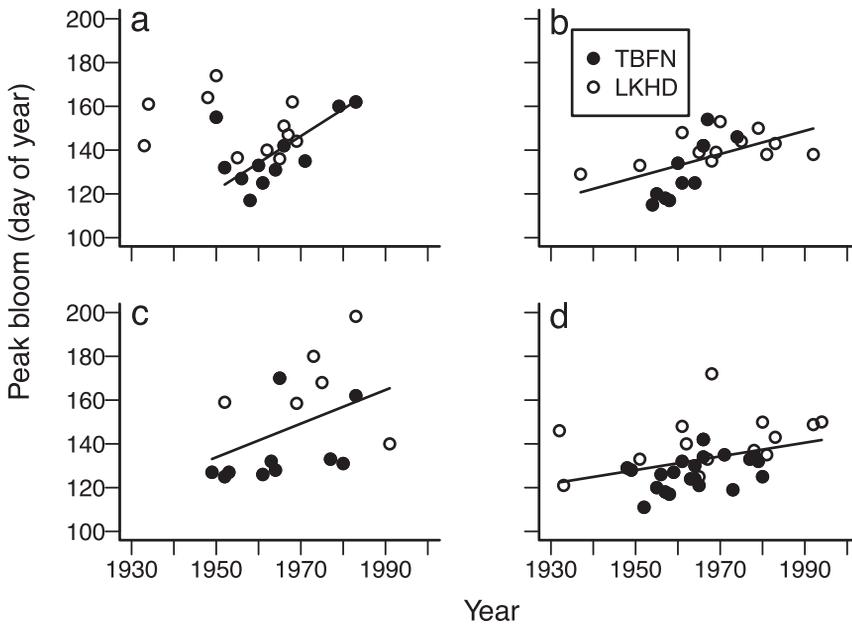
FIGURE 3. Plants in the Thunder Bay region, Ontario, Canada demonstrating significant positive changes in flowering phenology over time. a. Wood Anemone (*Anemone quinquefolia*), demonstrating a significant positive relationship from 1950–1983 only ($F_{1,15} = 20.4$, $P = 0.0004$, $r^2 = 0.58$, $\beta = 1.23$). b. Carolina Spring Beauty (*Claytonia caroliniana*, $F_{1,21} = 8.8$, $P = 0.007$, $r^2 = 0.3$, $\beta = 0.5303$). c. Wild Strawberry (*Fragaria vesca*, $F_{1,14} = 3.3$, $P = 0.092$, $r^2 = 0.19$, $\beta = 0.0051$ from log-transformed bloom date). d. Bloodroot (*Sanguinaria canadensis*, $F_{1,35} = 5.34$, $P = 0.027$, $r^2 = 0.13$, $\beta = 0.3125$). TBFN = data collected from the Thunder Bay Field Naturalists, LKHD = data collected from the Claude Garton Herbarium, Lakehead University.

relationship, but only with the exclusion of any observations made before 1950, which appeared distinctly separate from the distribution of the rest of the data series for that species (Figure 3a). There was a weak positive trend for Wild Strawberry ($F_{1,14} = 3.1$, $P = $ 0.098); applying a log-transformation improved the fit slightly (Table 4, Figure 3c). Collectively, the mean predicted peak bloom of the four species showing strong trends was delayed 35 days between 1932 and 2006. The other six species evaluated demonstrated

no significant trends (Table 2). Contrary to our predictions, no early blooming plants included in this dataset demonstrated a significant relationship of earlier blooming over the time series.

Across all species investigated, comparison of the LKHD and TBFN datasets in years when both were represented revealed that LKHD blooming dates tended to be nine days later on average than TBFN records ($t_{28} = 2.28$, $P = 0.03$).

Flowering as a function of sGDD₀

Yearly cumulative $sGDD_0$ was negatively related to peak flowering for four species evaluated (Table 4; Figure 4): Round-lobed Hepatica (*Hepatica americana* (de Candolle) Ker Gawler), Wood Anemone, Wild Strawberry, and Carolina Spring Beauty. Each of these species showed a significant negative trend with an increase in cumulative $sGDD_0$. With a higher quantity of cumulative thermal energy in spring, plants tended to have earlier peak blooms (Round-lobed Hepatica 24 days earlier; Wood Anemone 22 days earlier; Wild Strawberry 33 days earlier; Carolina Spring Beauty 18 days earlier). Collectively, the peak bloom of these species decreased a predicted mean of 21 days as cumulative $sGDD_0$ increased between 214 and 246 degree days.

Discussion

Changing phenology of the Thunder Bay region

Regardless of the analysis applied (either simple regression of flowering over time or response to $sGDD_0$), several angiosperms in the Thunder Bay region of northwestern Ontario were observed to have changed their flowering times in a consistent and predictable fashion in response to a warming climate. However, these metrics showed a perceived conflict in trend direction. In analyses that examine only changes in peak flowering over time, species showing a significant trend were unexpectedly observed to delay their flowering over time rather than advancing bloom time as we originally hypothesized. In contrast, but matching expectations, we observed earlier blooming with a greater accumulation of $sGDD_0$.

Trends in flowering phenology

Contrary to the trend we expected—earlier blooming periods with warmer springs—each of the species showing significant relationships reached peak bloom later in the year rather than earlier, from anywhere between 19 and 52 days (Wood Anemone and Wild Strawberry, respectively) over the entire time period evaluated. Of the four species that flowered later through time, Bloodroot and Carolina Spring Beauty
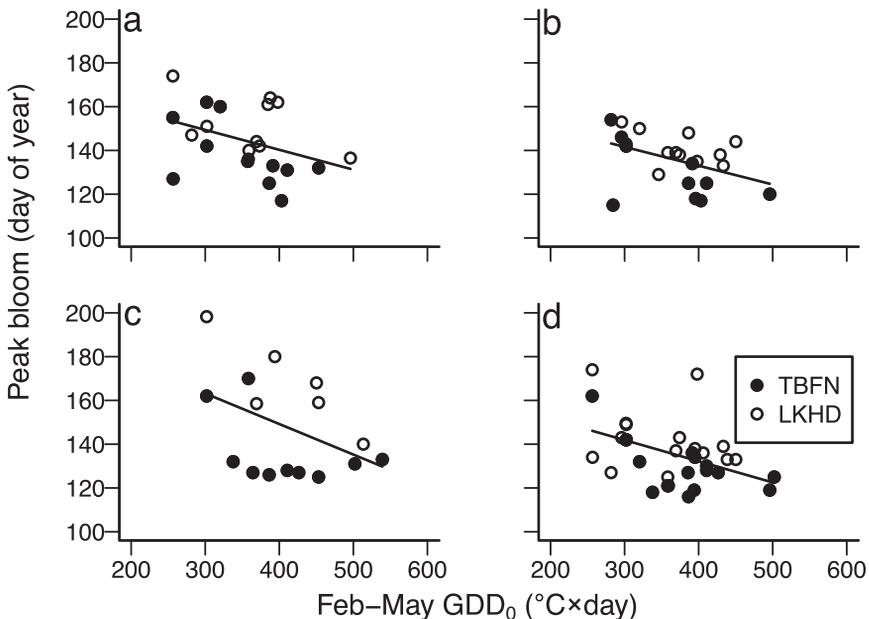
FIGURE 4. Plants in the Thunder Bay region, Ontario, Canada demonstrating significant negative changes in flowering phenology with growing degree days >0°C between February and May. a. Wood Anemone (*Anemone quinquefolia*, $F_{1,20} = 3.54$, $P = 0.08$, $r^2 = 0.15$, $\beta = -0.985$). b. Carolina Spring Beauty (*Claytonia caroliniana*, $F_{1,21} = 5.08$, $P = 0.035$, $r^2 = 0.2$, $\beta = -0.0860$). c. Wild Strawberry (*Fragaria vesca*, $F_{1,14} = 3.25$, $P = 0.09$, $r^2 = 0.19$, $\beta = -0.1396$). d. Round-lobed Hepatica (*Hepatica americana*, $F_{1,30} = 7.44$, $P = 0.011$, $r^2 = 0.2$, $\beta = -0.0968$). TBFN = data collected from the Thunder Bay Field Naturalists, LKHD = data collected from the Claude Garton Herbarium, Lakehead University.

flower briefly before tree leaf-out (Vezina and Grandt- ner 1965; Schemske 1978), whereas Wild Strawberry and Wood Anemone have longer flowering periods that continue after the canopy closes (Swink 1952; Eriksson and Ehrlén 1991). The delay in flowering for these species varies, with Carolina Spring Beauty and Bloodroot changing by 0.5 to 0.3 days per year, respectively (five to three days per decade) and Wood Anemone and Wild Strawberry delaying their flow- ering by 1.2 days per year (~12 days per decade over the period observed). These four plants are among the earliest flowering vascular plants seen in the Thunder Bay area (Table 3).

Other published work has noted species with conflicting trends over time. While the majority of published studies record earlier flowering times in response to warming temperatures, a minority of pre- vious studies have recorded delayed or no change in flowering for some species, particularly in response to warm fall or winter temperatures (Sherry *et al.* 2007; Hart *et al.* 2014). Additionally, while some species do not shift their first flowering or peak bloom, last flow- ering may be delayed (e.g., CaraDonna *et al.* 2014; Parmesan and Hanley 2015). Although no trends are detected for some of the species included in our data- set, it is possible that their response to changing cli- mate is not occurring with peak flowering but rather with delayed onset of the last bloom, fruiting periods, or senescence, which we were unable to evaluate in our study with the data available.

It is possible that the delay in flowering noted here could also be the result of a plastic response to win- ter temperature, specifically vernalization, a process through which overwintering plants use cold tem- perature cues to time their flowering (Williams *et al.* 2015). Vernalization is cumulative, so that the num- ber of days below a certain temperature must be met before the angiosperm responds to warm tempera- tures by flowering. During winters that have mild mean temperatures, plants that rely on this process will not meet their cumulative cold degree require- ments to respond to an earlier spring with a delay in their flowering time. Indeed, warming mean annual temperatures in northwestern Ontario and across Can- ada are largely attributable to warmer winters (Guzzo *et al.* 2017; Myers-Smith *et al.* 2019). Non-significant results for species included in our dataset could be the result of vernalization requirements not being met, as demonstrated in the analysis by Cook *et al.* (2012) of temperate early-flowering plants in the United King- dom. However, the conflicting trends we report with $sGDD_0$ regressions, along with lack of research con- ducted on the vernalization of native North Ameri- can plants, make it difficult to conclusively say that a cold winter temperature threshold is a requirement

of the plants included in our study. Further, of the 11 species assessed, four species of three different fam- ilies—three of which show delayed flowering in the simple temporal regression—showed a response to an increased number of growing degree days above 0°C; Wood Anemone, Round-lobed Hepatica, Wild Straw- berry, and Carolina Spring Beauty all reached an ear- lier peak bloom with a greater accumulation of $sGDD_0$.

While early North American studies of local phe- nology largely sought to characterize the timing of flowering over short timescales (e.g., Swink 1952; Vezina and Grandtner 1965), researchers now have the ability to examine long-term trends over larger timescales in accordance with climate data. Here, we see that the inclusion of GDD provides evidence consistent with predictions, and context for an oth- erwise surprising result when considering tempo- ral trends only. The similarity of significant trends among species suggests that the patterns observed are real and not spurious. Our results suggest that using metrics (e.g., temporal trends alone) that do not also consider biological responses to environmental cues may result in incorrect inferences. While later flow- ering in these species may be evidence of vernaliza- tion, data required to evaluate this possibility are lack- ing. Instead, our predicted results of earlier blooming with $sGDD_0$ are consistent with expectations due to increased thermal accumulation.

In the species that show significant but conflict- ing trends in temporal and $sGDD_0$ analyses, other work shows that when temperature is accounted for, these species bloom earlier in response to warmer climate. For example, Wood Anemone has flowered increasingly earlier in the southern part of its range, in conjunction with mild winters (Abu-Asab *et al.* 2001; Panchen *et al.* 2012). Canadian populations of another early-flowering species in the same family, Prairie Pasqueflower (*Pulsatilla nuttalliana* (de Can- dolle) Berchtold ex J. Presl), similarly showed a two- day decrease in flowering per decade in conjunction with thermal time models (Beaubien and Hamann 2011a). Carolina Spring Beauty shows similar sensi- tivity to earlier springs. Previously, only one study has examined the Canadian phenology of Carolina Spring Beauty, but without accounting for the influence of temperature (Vezina and Grandtner 1965). However, spring beauty (*Claytonia* spp.) is a North American genus that has demonstrated earlier blooming time with correspondingly early snowpack melt (Panchen *et al.* 2012; Gezon *et al.* 2016). Although snow melt data were not available for analysis in our study, oth- ers have demonstrated its correlation with earlier flow- ering times, especially in plants reliant on this abiotic factor as a primary cue (Lavoie and Lachance 2006; Lambert *et al.* 2010; Bjorkman *et al.* 2015).

The consistent but conflicting trends and non-responsiveness of some species we observed could also be the result of small sample sizes. Panchen *et al*. (2012), studying changing phenology of plants in the Philadelphia region, found that for the 150-year span of their study, species with short flowering periods showed significant results with 60 observations, while longer flowering species required up to 100 observations to show significant changes. When assessing TBFN and LKHD data together, the average number of observations per species was 50, which is slightly below both these thresholds. However, the species which showed significant trends for temporal or temperature-based analyses all had between 31 (Wild Strawberry) and 62 (Bloodroot) observations, indicating that despite smaller sample sizes of peak flowering records, there is still a strong enough trend to detect consistent changes in phenology. Species that did show significant phenological responses also varied in bloom period, from short- to longer-blooming periods. This suggests that there are other dynamics influencing the response of these plants.

It is also possible that some of the differences we observed are population-level adaptations or a plastic species response to differences in climate, where some populations have become more attuned to vernalization or temperature cues than others (Panchen *et al.* 2017; Prevéy *et al*. 2017). However, studies of phenology across native ranges of North American vascular plants do not regularly address differences in flowering time by populations. Additionally, many range oriented studies focus on expansion, contraction, or shifts, but have not examined the *in situ* differences between existing populations. Of the few studies that have addressed phenological differences at a latitudinal gradient, significant differences in requirements for germination and flowering have been observed, with more northern populations achieving smaller size and flowering earlier, compared to more southern populations achieving larger size and later flowering (van Dijk *et al*. 1997; Weber and Schmid 1998; Olsson and Ågren 2002). Here, what evidence of population level plasticity does exist is also conflicting; while many vascular plants readily respond to temperature cues (Nicotra *et al*. 2010; Schmidt *et al*. 2012; Tansey *et al*. 2017), others demonstrate no appreciable differences (Vitasse *et al*. 2009; Phillimore *et al*. 2012). It is evident that additional studies examining population-level phenological plasticity are necessary to tease apart these trends.

Importance of climatic metrics in local phenology studies

While climatic variables are important in characterizing phenology, the choice of environmental cue should be based on the life history of the organisms under consideration. Other approaches include snow melt (Lavoie and Lachance 2006), air temperature and moisture (Reed *et al*. 2019), and year-to-year climatic variability (Büntgen *et al*. 2012). Given that climatic effects vary over latitude and ecosystem, any of these metrics may provide an avenue to measure changes in flowering phenology and should be used in conjunction with phenological studies when such data are available. However, although a variety of approaches can be taken, GDD (sometimes referred to as thermal time models) does show consistency in the ability to predict the change over time for several thermally-dependent organisms across a broad range of taxa (Bonhomme 2000; Beaubien and Hamann 2011b; Lester *et al*. 2014). Additionally, understanding general flowering trends with GDD for early blooming species (Table 3) provides metrics for evaluating other phenological patterns across latitudinal gradients (Ross *et al*. 2021).

Source data

Without the combination of both locally collected field-naturalist observations and the herbarium records included in our study, sample sizes were too small to reveal reliably significant trends for all 11 species. Although many previous studies have included citizen science projects conducted over the short-term, the incorporation of long-term field-naturalist records to either augment existing data or as a data source on their own is still a relatively new practice (Miller-Rushing *et al*. 2012). As herbaria and museums become increasingly digitized, the combination of these two data sources has the potential to greatly expand our understanding of how biota respond to global climate change. While many studies of phenology attempt to cover large areas (Lavoie and Lachance 2006; Panchen and Gorelick 2017) or include thousands of specimens (Gordo and Sanz 2005; Hart *et al*. 2014), these types of studies often require vouchers from other herbaria or other records to bolster their datasets. For small herbaria, augmenting voucher data with naturalist observations may go further to reveal the responses of local ecosystems to climate that may otherwise go unnoticed.

Interestingly, in years when both TBFN and LKHD records were available, bloom times in the LKHD vouchers were nine days later on average than TBFN flowering times. It is unclear why this might be. Regardless, the delays in blooming reported here are all longer than nine days over the periods investigated, suggesting that the trends observed were real and unlikely an artefact of systematic differences between datasets. Further, the distribution of data from both datasets in species that demonstrate trends does not appear to be biased over the time periods investigated (Figure 3), further reducing the

possibility that bias in datasets might be contributing to observed results.

Our study suggests that field-naturalist data can contribute to long-term, ongoing studies of phenology. Current projects, such as the USA-National Phenology Network (USA-NPN), use citizen scientist data to track phenological change across North America, as well as archival datasets that are accessible to both researchers and the public (https://www.usanpn.org/results/dataset-list). These retroactive contributions to monitoring projects can help strengthen trends across time and space for researchers who are concerned with changing phenological norms. Additionally, they also can help to increase data coverage in areas where there may be few collections but written personal or organizational records exist.

Conclusion

While climate change is a global phenomenon, the impacts are felt locally. Our study demonstrates the value of both regional herbaria and long-term field-naturalist records in helping reveal the effects of climate change on a local level, and for the first time, uses data collected in the northwestern Ontario region to determine how vascular plants are responding to changing climate. We found that a small number of early-flowering vascular plants showed a response to warming seasons, but also that these trends oppose one another in temporal and climatic analyses. Lastly, our study supports the maintenance of local herbaria and the continuance of field-naturalist observations as essential resources for local phenological studies. Recording local phenological changes also provides a unique opportunity for institutions (such as herbaria) to partner with the public. Phenology is an accessible field: records are easy to keep for those without scientific training, allowing researchers, citizen scientists, and other organizations to work together to interact with, monitor, and manage their surrounding ecosystems.

Author Contributions

Acknowledgements

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SUPPLEMENTAL MATERIALS:

FIGURE S1. Collections per decade for all species included in the study for both the Thunder Bay Field Naturalists (TBFN) and Claude Garton Herbarium (LKHD) datasets.

TABLE S1. Voucher table for all Claude Garton Herbarium and Thunder Bay Field Naturalists specimens and observations used in this study.

TABLE S2. Climate data used to evaluate phenological changes in spring blooming perennials.

The Canadian Field-Naturalist

Parasitism and brood mortality in Alfalfa Leafcutting Bee (*Megachile rotundata* (Fabricius)), nesting in vacated comb cells of European Paper Wasp (*Polistes dominula* (Christ))

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Abstract

Social paper wasps (Hymenoptera: Vespidae) construct comb nests of tens to hundreds of brood cells that are abandoned each year before winter. The nests are positioned where they are protected from inclement weather and may remain intact for several years. Here, I detail observations of nests provisioned by the non-native, solitary Alfalfa Leafcutting Bee (*Megachile rotundata* (Fabricius, 1787); Hymenoptera: Megachilidae) in individual brood cells in vacated combs of the invasive, social European Paper Wasp (*Polistes dominula* (Christ, 1791)) on a green roof in Toronto, Ontario. A total of 12 paper wasp combs were dissected and 280 *M. rotundata* nests (one per wasp comb cell) were recovered; 22 nests were provisioned in 2013 consisting of 32 individual *M. rotundata* brood cells. Parasitism by *Melittobia* and *Monodontomerus* wasps accounted for 46.9% of *M. rotundata* mortality in the cells in 2013; mortality from all causes, including parasitism, was 78.1%. In contrast, total mortality of *M. rotundata* in brood cells provisioned in a human-made bee nest box on the same roof in 2013 was 4.2% and there was no parasitism. Mortality by parasitism and total brood mortality in 391 brood cells provisioned in 41 nests in the bee nest box in 2011–2013 were 2.0% and 21.2%, respectively. Therefore, the use of vacated paper wasp comb cells resulted in an overall >20-fold increase in parasitism and >3-fold increase in brood mortality over that observed in the bee nest box when all years are combined.

Key words: Megachilidae; Vespidae; non-native; invasive; parasitoids; urban ecology; bee nest box

Introduction

Alfalfa Leafcutting Bee (*Megachile rotundata* (Fabricius, 1787); Hymenoptera: Megachilidae) is one of the most widely distributed and economically important solitary bees in the world (Pitts-Singer and Cane 2011). Introduced into North America and subsequently established in the late 1930s (Stephen 1961; Mitchell 1962), its utility as a managed commercial pollinator has blossomed since the 1960s (Stephen and Torchio 1961). It now exists as feral populations throughout the continent and its ubiquity is most pronounced in urban and agricultural areas where it visits a variety of flowering species.

Megachile rotundata has immense flexibility in its use of nesting materials and cuts leaves from a wide range of plants (MacIvor 2016), sometimes flower petals (Klostermeyer and Gerber 1969), and even plastic shopping bags (MacIvor and Moore 2013) to enfold and partition brood cells. Each brood cell in a nest contains an individual egg on top of a ball of pollen and nectar provided by the female. The bee is also flexible in where the nest is constructed. As an aboveground "renter", *M. rotundata* is a cavity-nester with females searching for holes excavated by beetles in wood or hollow plant stems (Pitts-Singer and Cane 2011). It will also nest in a variety of human-made materials, such as plastic straws (Stephen and Every 1970), polystyrene boards (Richards 1978), or rolled paper tubes (Sheffield *et al.* 2008) and has even been found in the radiator of an antique tractor (Sheffield 2017).

Interest in the management of *M. rotundata* populations for pollination services, or simply as a hobby, has increased dramatically with the development and retailing of human-made bee nest boxes (MacIvor 2017). The boxes are made of pre-formed horizontal cavities of a variety of materials (e.g., holes drilled into wood, bundled hollow plant stems, or rolled paper and cardboard tubes) that provide nesting cavities for *M. rotundata* and other solitary bee and wasp species to lay and provision their eggs (Krombein 1967; Tscharntke *et al.* 1998; Sheffield *et al.* 2008;

Staab *et al.* 2017). *Megachile rotundata* will readily nest in aggregated conditions; thus, tens to thousands of cavities may be grouped together. Further, females are attracted to previously used nests, so large populations are possible (Pitts-Singer 2007).

While inspecting a bee nest box on a green roof at York University campus in Toronto, Ontario, I discovered ~20 vacated comb nests constructed by the invasive, social European Paper Wasp (*Polistes dominula* (Christ 1791); Hymenoptera: Vespidae) on the underside of awnings of vaulted windows along the inner perimeter of the roof. The paper wasp nests consisted of exposed combs of unenveloped, vertically oriented cells and were located in places protected from inclement weather (Downing and Jeanne 1986). *Polistes dominula* has spread throughout North America, displacing native wasps, and the species is common in cities (Cervo *et al.* 2000), where food resources are abundant and buildings provide shelter (Höcherl and Tautz 2015). The paper comb nests are vacated by the wasps after one year but, if protected, the structure may remain for several more. On close inspection, I noticed that many of the paper wasp comb cells were being used as nesting cavities by leafcutting bees (Figure 1a–c). Hundreds of comb cells contained individual nests made by *M. rotundata*, which have a distinct small size and brood cell construction pattern compared with other leafcutting bees in the region.

Here, I describe the results from dissecting these paper wasp combs and compare the survival, parasitism, and brood mortality of the *M. rotundata* nests found in the paper wasp comb cells with those from a nearby bee nest box on the same building.

Methods

In July 2013, 12 individual vacated paper wasp combs that contained *M. rotundata* nests were dissected. The combs were located on the fourth-storey roof of York University's Computer Science Building (43°46′26.24″N, 79°30′18.73″W), which is northwest of downtown Toronto, Ontario. The unirrigated green roof was originally seeded in 2001 (for details, see Toronto and Region Conservation Authority 2006) and is a mix of extensive (<15 cm substrate depth) and intensive (>15 cm) growing media substrates. Flowering plants included in the original seed mix, such as Lance-leaved Tickseed (*Coreopsis lanceolata* L., Asteraceae), False Sunflower (*Heliopsis helianthoides* (L.) Sweet, Asteraceae), Foxglove Beardtongue (*Penstemon digitalis* Nuttall ex Sims, Plantaginaceae)*,* and Black-eyed Susan (*Rudbeckia hirta* L., Asteraceae), persist on the roof. Many other flowering plants have arrived spontaneously, including Common Milkweed (*Asclepias syriaca* L., Apocynaceae)*,* Annual Fleabane (*Erigeron annuus* (L.) Persoon, Asteraceae), White Sweet-clover (*Melilotus albus* Medikus, Fabaceae)*,* Tall Goldenrod (*Solidago altissima* L., Asteraceae)*,* White Clover (*Trifolium repens* L., Fabaceae)*,* and Common Dandelion (*Taraxacum officinale* F.H. Wigg., Asteraceae).

All *M. rotundata* nests (one nest per paper wasp comb cell) in the 12 combs were dissected and determined to be either provisioned pre-2013 or in 2013.
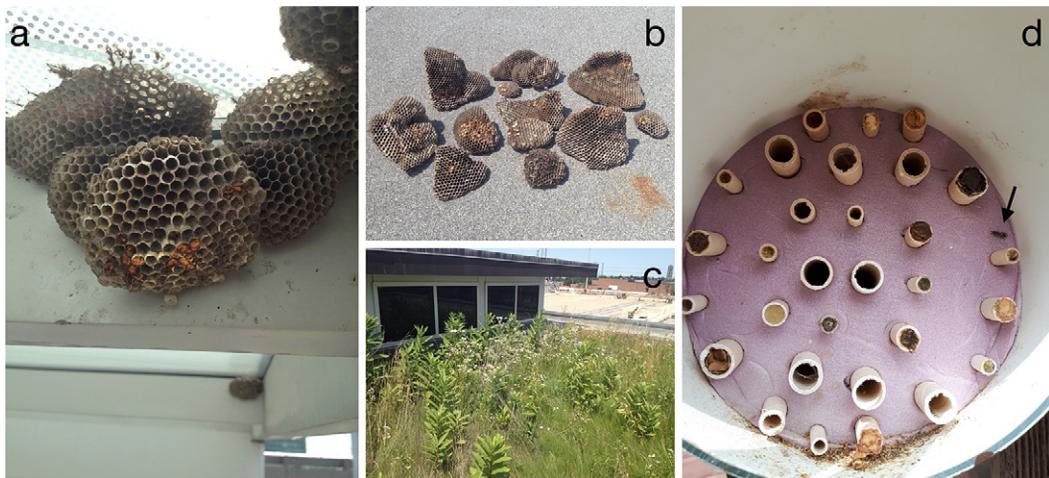
FIGURE 1. European Paper Wasp (*Polistes dominula*) combs and an example of the bee nest box on a fourth-storey green roof in Toronto, Ontario, Canada. a. Vacated unenveloped paper wasp comb cells where provisioned Alfalfa Leafcutting Bee (*Megachile rotundata*) nests were observed. b. A collection of paper wasp nest combs with *M. rotundata* nests visible. c. The green roof where the observations were made. d. Example of the bee nest box from which *M. rotundata* were obtained for comparison, with parasitoid *Monodontomerus* present (arrow). Photos: a–c. J.S. MacIvor. Photo: d. Kathy Bosci.

Those presumed to be provisioned before 2013 were mouldy and decomposed and sometimes contained the remnants of a dead larva or an emergence hole indicating that a bee or parasitoid(s) had matured and left the nest; these were not included in further analyses. Nests provisioned in 2013 with one or more brood cells containing uneaten fresh pollen or a living bee larva or parasitoid(s) were included in my analysis. Uneaten pollen can include a shrivelled early instar larva indicated that the nest cell had failed (e.g., Danks 1971).

Living larvae suspected to be *M. rotundata* were individually stored in 24-well assay trays at room temperature, moved to a 4°C refrigerator to simulate late-fall and winter (October–April), and then to 26°C and 60–65% humidity in spring until emergence. Adult female and male bees were identified using Sheffield *et al.* (2011).

Parasitized nest cells were also collected, and the parasitoids allowed to pupate. Adults were identified to either genus *Melittobia* Westwood, 1848 (Hymenoptera: Eulophidae) or *Monodontomerus* Westwood 1833 (Hymenoptera: Torymidae) using the dichotomous key in Peck (1969). No vouchers were collected so identification to species is not possible. Both parasitoid wasp taxa are gregarious and multivoltine. Mated females use olfactory cues to locate a prepupal bee in its brood cell, sting it, then lay eggs externally on the host surface (Eves 1970; Matthews *et al.* 2009). *Melittobia* are small (1.0–1.5 mm in length) and must gain entry inside the brood cell to access the host, whereas *Monodontomerus* (2.0–4.0 mm) may insert their ovipositor through the brood cell (Eves 1970). Larvae hatch from eggs quickly and begin to feed on the immature bee, emerge as adults, then chew through the brood cell ready to attack other immature bees in a nest or aggregation (Farkas *et al.* 1985; Matthews *et al.* 2009).

A bee nest box (Figure 1d) on the same green roof was part of a larger study detailed in MacIvor and Packer (2015). From it, 30 horizontally oriented cardboard nesting tubes of three widths (3.4 mm, 5.5 mm, and 7.6 mm), all 15 cm long, were useable by *M. rotundata* (although the 5.5 mm tubes were used primarily). All specimens from nesting tubes were reared to adults (as above), identified to species, and the number of failed (e.g., mouldy, shrivelled) and parasitized brood cells counted. Representative vouchers of *M. rotundata* from the bee nest box for all three years are curated in the Biodiversity of Urban Green Spaces (BUGS) lab at the University of Toronto Scarborough (2011-163A6, 2012-303B1, and 2013-307C2).

Brood mortality was defined as the sum of the number of brood cells that failed because they were parasitized or from other causes.

Results

The 12 dissected paper wasp combs yielded 280 *M. rotundata* nests constructed in downward facing (i.e., vertically oriented) cells (Figure 1a). From this total, 258 nests were determined to be provisioned pre-2013 and each contained an unknown number of brood cells per nest. Only 22 *M. rotundata* nests consisting of 32 brood cells (average 1.5 brood cells/ nest cell, reflecting the depth of each comb cell ~3 cm) could be confirmed as having been provisioned in 2013 (Table 1) and were retrieved from five separate paper wasp combs. Seven larvae in these 32 brood cells survived to adulthood (two female, five male), 15 were parasitized by *Monodontomerus*, and 10 perished because of mould or other unknown causes (e.g., disease/virus; Table 1). The average (± SE) number of parasitoids per parasitized brood cell was 4.4 ± 1.7. No *Melittobia* were found in the paper wasp combs. Dermestid (*Trogoderma*) beetles (Coleoptera: Dermestidae) were also recovered from three paper wasp combs and near (or in) former *M. rotundata* nests, indicating that they may have scavenged on the remains of pollen provisions and immature bees (Bohart 1972).

From the bee nest box, 41 *M. rotundata* nests (one nest per nesting tube) consisting of 391 brood cells

TABLE 1. Number of nests and brood cells provisioned, as well as survival, parasitism, and failure of Alfalfa Leafcutting Bee (*Megachile rotundata*) in European Paper Wasp (*Polistes dominula*) comb cells and in a bee nest box on a fourth-storey green roof in Toronto, Canada.

Nest type	Year	No. nests	No. brood cells	Average no. brood cells/ nest	Brood outcome, no. (%)		
					Survival to adult	Parasitized	Mould/failed
Paper wasp comb	2013	22	32	1.5	7 (21.9)	15 (46.9)	10 (31.2)
Nest box	2011	13	186	14.3	121 (65.1)	0 (0.0)	65 (34.9)
	2012	20	181	9.1	166 (91.7)	8 (4.4)	7 (2.2)
	2013	8	24	3.0	21 (87.5)	0 (0.0)	3 (4.2)
	All years combined	41	391	9.5	308 (78.8)	8 (2.0)	75 (19.2)

were recorded in 2011–2013, with an average of 9.5 brood cells/nest (Table 1). In 2013, none of the 24 brood cells in eight nests was parasitized, but three failed as a result of unknown causes. In 2011, 13 nests contained 186 brood cells, of which 121 survived, 65 failed, and none was parasitized. In 2012, I recorded 20 nests containing 181 brood cells: 166 survived to adulthood, seven failed, and eight were parasitized by either *Melittobia* ($n = 5$) or *Monodontomerus* ($n = 3$).

The number of *M. rotundata* in the bee nest box fluctuated among years presumably because of competition for nesting opportunities with other species. For example, the number of *M. rotundata* nests was lower in 2011 and 2013 than in 2012 because the spring-active and non-native Blue Mason Bee (*Osmia caerulescens* (L., 1758); Hymenoptera: Megachilidae) filled nesting tubes that would otherwise be available for summer-active species such as *M. rotundata*. There was no evidence of *O. caerulescens* nesting in paper wasp combs.

Altogether, parasitism and brood mortality occurred >20 and >3 times more often, respectively, in *M. rotundata* brood cells provisioned in the paper wasp combs compared with the bee nest box.

Discussion

The observations reported here confirm the nesting flexibility that others have shown for *M. rotundata* (e.g., Stephen and Every 1970; Richards 1978; Sheffield *et al.* 2017) and demonstrates that the species can also opportunistically use vacated *P. dominula* paper wasp comb cells as nesting cavities. However, the rates of parasitism and brood mortality were higher in the paper wasp combs than in a nearby bee nest box, at least during one year on one green roof in Toronto.

Many leafcutting bees nest in pre-existing cavities in wood or hollow dried plant stems; thus, parasitoids are often restricted to penetrating the nest only through the front entrance. The high rates of parasitism in *M. rotundata* I found in the paper wasp combs may be a result of *Monodontomerus* being able to access bee larvae directly through the thin paper cell walls. Krombein (1967) found that the frequency of ovipositor insertion by parasitoid wasps from outside the cavity into a solitary bee brood cell declined when cavity walls were >2 mm thick. As well, paper wasp comb cell walls may be further weakened and accessible to parasitoids because in sheltered locations (e.g., under a roof awning), *P. dominula* will allocate less protein to paper construction (for waterproofing and strengthening) and more to developing larvae, compared with less-sheltered sites (Curtis *et al.* 2005). Nesting in paper wasp comb cells may represent a habitat sink (Delibes *et al.* 2001) where environmental cues used by *M. rotundata* to differentiate good

versus bad nest sites fail and some suffer reduced reproductive fitness as a result. Nest site fidelity, gregarious nesting behaviour, and the "scent" of used nests might attract subsequent *M. rotundata* (Parker *et al.* 1983), enhancing the consequences for these bees.

Although several *M. rotundata* adults emerged successfully from the paper wasp comb cells, brood mortality (parasitized plus failure from all other causes) was higher than in the bee nest box (Table 1). Because nesting tubes in the box are arranged horizontally, eggs are laid on pollen masses on a lateral surface. In the paper wasp combs, cells are vertical or almost so; thus, the provisioned bee eggs could have been laid on the downward facing side of a pollen provision possibly leading to increased mortality if bee larvae fall off the provision. It is typically recommended that bee nest boxes not be moved during a season, as handling may cause mortality (Minckley and Danforth 2019). There may be other examples of natural nest cavities oriented at different angles, but it is unknown whether this increases mortality. Bee nest boxes may enhance reproductive fitness of bee species that accept them, allowing local populations to grow (Steffan-Dewenter and Schiele 2008). Whether bee nest boxes serve as a conservation tool for native bees in urban areas requires more scrutiny given the large number of non-native bees (*M. rotundata* and *O. caerulescens*) produced from this one nest box on a building rooftop.

Vacant paper combs of *P. dominula* are common in urban areas and represent a unique and understudied microhabitat for arthropod communities. Native solitary cavity-nesting wasps, including *Euodynerus foraminatus* (de Saussure) (Hymenoptera: Vespidae), *Parancistrocerus fulvipes* (de Saussure) (Hymenoptera: Vespidae), *Trypoxylon clavatum* Say (Hymenoptera: Crabronidae), and *Auplopus mellipes* (Hymenoptera: Pompilidae; Rau 1944 [first two species], 1928 and Evans 1953, respectively), as well as native solitary cavity-nesting bees such as Blue Orchard Bee (*Osmia lignaria* Say; Hymenoptera: Megachilidae) and *Osmia cordata* Robertson (Hymenoptera: Megachilidae; Rau 1937 and 1928, respectively), have been reported nesting in the vacated comb cells of native paper wasps in non-urban areas. One study in the United States compiled a list of 42 species in 28 invertebrate families that are parasites or symbionts of native *Polistes* and use vacated paper wasp combs as habitat (Nelson 1968), yet no description of *M. rotundata* or other *Megachile* nesting in paper wasp comb cells are present in the literature. However, online images exist (e.g., Prouty 2010) and suggest that the observations documented here may not be an isolated occurrence.

The unusual nesting behaviour I document emphasizes how little we know about the generality and specificity of nesting in solitary wild bees. Others have characterized nesting conditions for various bee species to better understand habitat preferences (e.g., Cane 1991; Sardiñas and Kremen 2014; Antoine and Forrest 2020; Harmon-Threatt 2020), but continued documentation and observation are needed, even for widespread species such as *M. rotundata* that have immense flexibility in nesting requirements. This is critical for implementing design (e.g., bee nest boxes) and management (e.g., removal of invasive paper wasp combs) in urban areas that support the nesting requirements of native bees and do not inadvertently enhance introduced species (Russo *et al.* 2021).

Acknowledgements

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The Canadian Field-Naturalist

Note

Apparent winterkill of Painted Turtle (*Chrysemys picta*)

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Abstract
Around the margin of an artificial pond in Ottawa, Ontario, we found 25 Painted Turtles (*Chrysemys picta*) that appeared to have died over the course of two winters (17 during the first winter and eight during the second). We examined meteorological data to try to determine the cause of the mortality. Summer and fall rains were only slightly below normal in both years, suggesting water levels should have been close to normal. The winter air temperature was warmer than normal and winter snowfall was slightly above normal in both years. Unseasonable weather does not appear to be responsible for the winter mortality and the pond's maximum depth of 1.7 m should prevent freezing to the bottom. It is possible that the artificial nature of the pond creates suboptimal overwintering habitat, rendering the site an ecological trap; however, there is no direct evidence to support this theory. It is also possible that winter mortality of turtles is widespread at temperate wetlands, but that dead turtles were more detectable at this site because of the bare shoreline around the pond. Winter mass mortality events, if common, may represent an additional threat to turtle populations, which are declining from various anthropogenic threats.

Key words: Winterkill; Painted Turtle; *Chrysemys picta*; mortality

Freshwater turtles must spend the winter in a state of periodic or continuous inactivity in most temperate locations. This inactive state has been called hibernation or brumation, but, more generically, it has been termed overwintering, because the behavioural and physiological states vary among turtles (Ultsch 2006). In northern latitudes, turtles may spend half the year overwintering under water (Ultsch 1989, 2006). Overwintering can be challenging and lead to death because of prolonged anoxia or freezing (Ultsch 2006). Mortality events can result in the death of many turtles. For example, 186 turtles from five species died when a pond froze to the bottom in Iowa (Christiansen and Bickham 1989), 144 turtles from four species died from freezing in three wetlands that dried up over the winter in Missouri (Bodie and Semlitsch 2000), 86 Painted Turtles (*Chrysemys picta*) died over the winter after water levels in a lake declined dramatically in South Dakota (Platt *et al.* 2008), and 56 Painted Turtles and three Blanding's Turtles (*Emydoidea blandingii*) died over the winter in a "large shallow pond" in Ottawa (Bleakney 1966). Reports of winterkill are valuable for assessing the frequency and magnitude of such mortality events and the factors that contribute to them.

On 28 July 2020, we found 17 dead Painted Turtles along the shoreline or in shallow water near the shore at a human-constructed pond in western Ottawa, Canada (45.43633°N, 76.02359°W). The pond did not exist before 2002, based on evidence from historical air photos (City of Ottawa 2022). The pond is not connected to any other water body; it is irregular in shape but has a total length of ~500 m, a width that varies from ~40 to 130 m, and a total area of ~3 ha. Based on measurements taken on 5 July 2021, the maximum depth of the pond is 1.7 m.

All 17 of the turtles found in 2020 had been dead for some time. In most cases, only the carapace and plastron were present, often with some scutes missing. The most intact turtles still had dried legs or a head present along with the shell. Some turtles were reduced to just fragments of the shell. In all cases, there were enough scutes still attached to the bone to identify them as Painted Turtles based on the presence of red markings on the scutes. Nine of the 17 turtles were relatively intact and were measured to the

nearest half centimetre. The median plastron length (PL) was 12 cm (range 10.5–13 cm). One turtle was identified as an adult female (10.5 cm PL), but none of the others could be sexed confidently. Two of the turtles were found in shallow water near the shore, while the rest were found on shore, typically within 1–2 m of the water, but up to 5 m from the pond edge. The bodies of the turtles were dispersed around the pond margin, up to ~300 m apart, although five turtles were found within a few metres of each other. Given the condition of the bodies, the turtles likely died several months before they were found. The most compelling evidence that the turtles died over the winter is a photo taken of a dead male Painted Turtle in the pond on 2 April 2020 (Figure 1). Its body is clearly intact and it was not killed by a predator. It is possible that some of the dead turtles in poorer condition may have died in the previous year, given how long it can take for turtle shells to disarticulate (Dodd 1995). It is unknown how large the Painted Turtle population in the pond is, although the largest number of individuals counted on one day was 15 on 30 May 2021.

We revisited the pond in spring 2021 to determine whether winterkill recurred and also received observations of turtles from others. Three live Painted Turtles were observed on 22 March when the pond was still mainly frozen over. The turtles were in open water at the shoreline, alive but sluggish. On 25 March, one live Painted Turtle (~10 cm PL) was found with ~90 leeches attached to the plastron and around the head. Two dead Painted Turtles were also found on this date. During 3–19 April, a total of six dead Painted Turtles were found, for a total of eight dead turtles in 2021. Five of the six were in the pond and the other was within ~1 m of the water. The sizes of the turtles, estimated from photographs, averaged approximately 10 cm PL (range 6–12 cm). One was an adult male, two were adult females, and the remainder were unsexed or juveniles. None of the turtles had any visible injuries.

Painted Turtle is one of the most anoxia-tolerant species of turtles (Ultsch 2006). In particular, the three northern subspecies can remain responsive for more than 150 days in anoxic water (Ultsch *et al.* 1985; Reese *et al.* 2004). Under hypoxic conditions, Painted Turtles may seek out colder areas of a water body to delay metabolic acidosis (Rollinson *et al.* 2008). Nonetheless, prolonged anoxia or freezing may cause mortality (Ultsch 2006), and untangling these two causes of death is often difficult because, when dead turtles are found in spring, the pond has already thawed. Monitoring turtles over the winter can confirm cause of death, as radio-tracking Painted Turtles in British Columbia resulted in finding one turtle frozen where lake ice reached the bottom in mid-winter (St. Clair and Gregory 1990).

FIGURE 1. Dead adult male Painted Turtle (*Chrysemys picta*) found in a pond in Ottawa on 2 April 2020. On this day, the air temperature reached a minimum of −1.4°C and a maximum of 10.8°C (Government of Canada 2020a). Photo: T. Hamar.

We examined meteorological data from the nearby Ottawa International Airport (~30 km southeast of the pond) to determine if weather factors could explain the observed winterkill. Precipitation from June to November 2019 and 2020 totalled 451.8 mm and 466.0 mm, respectively, which is slightly lower than the 30-year climate normal (1981–2010) of 528.3 mm (Government of Canada 2020a); however, it is likely pond water levels were near normal at the start of winter. Winterkill of Painted Turtles in South Dakota resulted after a drought when rainfall was 50% below normal (Platt *et al.* 2008).

The monthly mean minimum temperatures for December to March in both winters were on average 2.2°C (range 0.8–4.7°C) and 1.9°C (range −0.5–4.7°C) warmer, respectively, than the normal minimum temperatures (Government of Canada 2020a); thus, it seems unlikely that temperature was responsible for the mortality. A winterkill of Snapping Turtle (*Chelydra serpentina*) occurred in Ottawa when the monthly mean minimum temperature was on average 2.8°C colder than normal each month during the winter (Seburn 2015).

Lack of snow cover can substantially increase the seasonal freezing depth (Zhang 2005), but from November to February during both winters Ottawa received 169.9 cm and 164.5 cm of snow, which is slightly higher than the normal snowfall of 161.3 cm for that period (Government of Canada 2020a).

It seems unlikely that unusual weather conditions were responsible for the mortality of the turtles as conditions were close to average during both winters. It also seems unlikely that the entire pond froze to the bottom both winters, as the maximum depth is 1.7 m and Painted Turtles are known to overwinter in ponds only 1.3 m deep north of our study area (Rollinson *et al.* 2008) and often in areas of wetlands that are less than 0.5 m deep (Taylor and Nol 1989). Given that the pond is human-made, it is possible that basin characteristics create overwintering habitat that is not ideal. "Ecological traps", habitats selected by animals that reduce their fitness, have been widely documented, but most research has been on birds (Hale and Swearer 2016). Although the pond may form some kind of ecological trap, turtles are known to make use of artificial wetlands elsewhere in Ontario and successfully overwinter there (Dupuis-Desormeaux *et al.* 2018). It remains unclear what caused the winterkill over two consecutive winters, but it is possible that winterkill occurs in many temperate locations but dead turtles are rarely found or reported. The bare shoreline of this pond may make it easier to find dead turtles compared with wetlands with abundant shoreline vegetation.

Turtles face a wide range of anthropogenic threats and currently all eight species of freshwater turtles in Canada are listed as Species at Risk (Government of Canada 2020b). If winterkill in Canada is common and widespread, then turtle mortality rates may be higher than commonly thought. Chronic, ongoing adult mortality can have long-term effects on turtle populations. Two decades after a mass mortality event in Algonquin Provincial Park, for example, a population of Snapping Turtles has still not recovered (Keevil *et al.* 2018). Researchers are encouraged to report apparent winterkill of turtles to determine how common such events are at northern latitudes.

Author Contributions

Acknowledgements

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Status and declining trend of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) orchids in Pukaskwa National Park, Ontario, Canada

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Abstract
Pukaskwa National Park hosts part of a disjunct population of the perennial orchid species Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) on the north shore of Lake Superior, Ontario, Canada. Monitoring of *C. passerinum* within Pukaskwa National Park occurred between 1979 and 2019. During that period, the total number of stalks and the number of *C. passerinum* colonies within the park have declined, while the proportion of flowering stalks at colonies has increased. Although the number of stalks at extant colonies is stable, this population may be suffering from lack of recruitment and is at risk of extirpation. We hypothesize that the decline and lack of recruitment are a result of changing habitat conditions due to natural and anthropogenic influence.

Key words: Franklin's Lady's-slipper; Orchidaceae; Parks Canada; population decline; orchid conservation; dune succession; recruitment; climate change

Introduction

Sparrow's-egg Lady's-slipper (*Cypripedium passerinum* Richardson; Orchidaceae) is a perennial herbaceous orchid species distributed in boreal and subarctic regions of North America from Alaska to Hudson Bay and south to northern Montana (Sheviak 2002). Disjunct populations occur on the north shore of Lake Superior at the mouth of the Pic River and in the Mingan Islands near the north shore of the St. Lawrence River (Keddy *et al.* 1983; Rankou 2014).

The conservation status of *C. passerinum* is Secure globally (G5) and in Canada (N5) and is Apparently Secure (S4) in Ontario (NatureServe 2020). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has not yet assessed the species and therefore it cannot be considered for listing under the Canadian *Species at Risk Act*. In 2014, the species was added to the International Union for the Conservation of Nature (IUCN)'s Red List of Threatened Species as Vulnerable (Rankou 2014). The IUCN suggests that within the global range of this species (5 722 278 km²), there are 1200 to 10 000 mature individuals in 20 known locations, with an area of occupancy (the area within its extent of occurrence occupied by a taxon typically calculated by adding the number of occupied 2 km × 2 km grid squares) of 650 km² (Rankou 2014). This is likely a great underestimate dependent on the definition of location, as there were 105 sites of this plant mapped in the Northwest Territories (Porsild and Cody 1980), some likely overlapping with 28 sites in Ontario (Whiting and Catling 1986) and more than 50 sites in northwestern North America (Catling and Bennett 2007). Furthermore, there are likely additional unknown threats-based locations within the vast and botanically underexplored Hudson Bay Lowland (M.J. Oldham pers. comm. 11 September 2017). Human impacts, including deforestation, wildfire, tourism, urbanization, trampling, and plant collection for horticultural and medicinal use, may threaten the persistence of this species (Rankou 2014). However, much of the range occupies northern Canada, where there is relatively little human impact (M.J. Oldham pers. comm. 11 September 2017).

Pukaskwa National Park (PNP) encloses part of the disjunct population of *C. passerinum* on the north shore of Lake Superior, south of the mouth of the Pic River (48.6°N, 86.3°W), within an active cove dune system formed by glacio-fluvial deposits (Zoltai 1967; Bakowsky and Henson 2014). The

other part of this population occurs on land managed by Biigtigong Nishnaabeg (formerly Ojibways of the Pic River First Nation), north of the mouth of the Pic River. This disjunct population was discovered in the 1800s (Macoun 1888) and rediscovered in 1964 (Soper 1965). Keddy (1979) characterized the distribution, morphology, phenology, growth, reproduction, and habitat of this population. In 1979, the population consisted of 57 "colonies" that contained 1–137 (average 17) stalks of *C. passerinum* each and a total of 919 stalks (Keddy 1979); 443 stalks were within PNP. Colonies were clusters of stalks (that may be clones of one or more individuals) ≥1 m from other clusters, except in the case of three clusters, which were <1 m apart, recognized as groups because of obvious habitat differences (Keddy *et al.* 1983).

Following Keddy's (1979) study, PNP recognized *C. passerinum* as a rare plant within the park and established a management plan for this species, which included a monitoring program to quantify changes in the number of stalks over time and thereby assess the effectiveness of management practices (Parks Canada Agency 1986). Many unpublished monitoring reports of the status and trends of the colonies within PNP have been written (Keddy 1984; Vien 1985a,b, 1987,

1988, 1989, 1990; Vien and Mosquin 1986; Reside 1992, 1993; Irvine and Drake 2017a,b; Irvine and Patterson 2021). Here we document the status of *C. passerinum* in PNP in 2019 and discuss trends in the population observed from monitoring conducted since 1979. Specifically, we determined the trends in the number of plants in all colonies and in extant colonies only, the trend in the percentage of flowering stalks, and whether habitat conditions (slope, aspect, canopy cover, and cover of downed woody debris) differed between extant and extirpated colonies.

Species biology

Cypripedium passerinum is a rhizomatous, perennial herb, capable of asexual (clonal) reproduction and sexual reproduction via seeds (Figure 1). Aboveground stalks of *C. passerinum* are erect, 12–50 cm tall, with 3–7 elliptic-lanceolate leaves (5–19 × 1.5–6 cm) arranged alternately along the length of the hairy stem (Sheviak 2002). Flowering plants have one (rarely two) flowers with two lateral and one dorsal sepals, two lateral white petals, and one central basal petal forming a pouch with purplish spotting at the lip and inside. Individuals of *C. passerinum* can take up to 15 years to flower, which occurs in June and July (Keddy *et al.* 1983). The population of *C. passerinum*
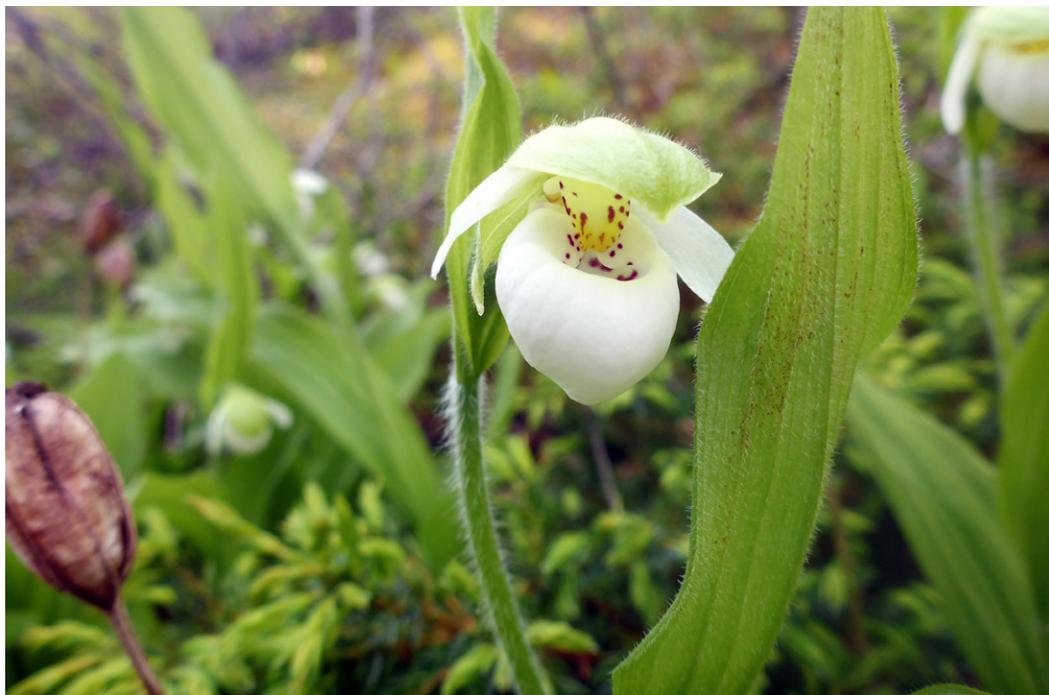
FIGURE 1. A flowering stalk of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) in Pukaskwa National Park in 2019. A cured seed pod, persistent from the year before, is visible in the left side of the photograph. Photo: Parks Canada Agency.

at the mouth of the Pic River is capable of self-pollination (Keddy 1979; Catling 1983; Catling and Bennett 2007); self-pollinated flowers produce seed pods (99% of healthy flowers produced seed pods; Keddy 1979), and seed pods (capsules) contain enormous numbers of lightweight seeds (Keddy 1979). *Cypripedium* spp. have specific requirements for seed germination, such as the presence of a symbiotic mycorrhizal fungus (Shefferson *et al.* 2005). If seed germination is successful, *Cypripedium* spp. must survive a subterranean protocorm life stage, relying on carbon production from their symbiont, to produce above-ground stalks (Curtis 1943; Shefferson 2006). Both vegetative and flowering stalks of *C. passerinum* can produce clonal offshoots along shallow-buried rhizomes, such that a large network of clonal stalks may eventually persist above-ground (Keddy *et al.* 1983) and may transition to and from periods of extended dormancy, as in other species of *Cypripedium* (Shefferson 2006). *Cypripedium passerinum* occupies a variety of habitats, including moist coniferous forests, thickets, forest openings, wooded ravines, littorals of streams, lakeshores, swamps, river terraces, edges of lakes and streams, and talus slopes in the montane and subalpine zones, on moist to dry substrates in bright light and on well-drained slopes (Sheviak 2002; Rankou 2014).

Methods

Monitoring

All colonies (clusters of stalks ≥1 m from other stalks; Keddy 1979) of *C. passerinum* in the population near the Pic River within and beyond PNP were identified in 1979 ($n = 52$) and given unique identifying numbers. All colonies within PNP ($n = 22$) were monitored annually from 1982 to 1990, and in 1992, 1993, 1999, 2001, 2016, 2017, and 2019. In 1983, PNP installed 13 permanent rebar stakes and recorded the directional distance between the nearest stake and *C. passerinum* colonies. This system was used to relocate the colonies in subsequent years until 2016, when the global positioning system coordinates of each colony was recorded. Surveys occurred between 16 July and 20 August of each year and consisted of counting the number of vegetative and flowering stalks at each colony. We used stalks (ramets) as a proxy for the number of individuals because the number of genets (true genetic individuals) within a colony could not be identified without soil excavation (Gregg 2004). Beginning in 1982, stalks at colonies 45–47 were combined into one colony (identified as colony 45-46-47 and considered one colony hereafter), as were stalks at colonies 50 and 51 (identified as colony 50-51 and considered one colony hereafter), for an unrecorded reason. In 1983, one additional

colony (53) was found. Thus, we consider the historical number of colonies in PNP to be 20.

In 2019, we estimated the slope of the ground and directional aspect of the slope using a handheld compass, and we estimated the overstorey canopy cover and amount of downed woody debris in a ~1 m² area, or the area occupied by plants (mean = 1 m × 0.5 m), in four categories (0–24, 25–49, 50–74, 75–100%) at historical and extant colonies.

To determine the general trend of the *C. passerinum* population in PNP, we tested whether the number of *C. passerinum* stalks had increased, decreased, or remained stable between 1970 and 2019. We used a generalised additive model with a negative binomial error distribution to account for non-linearity, serial autocorrelation, and overdispersion in the count data (Wood 2011). Stalks within four colonies were excluded in the total count as these colonies were not surveyed every year, either to avoid trampling Northern Twayblade (*Neottia borealis* (Morong) Szlachetko; Keddy 1984) or because the nearest rebar stakes were not found (Irvine and Drake 2017).

To determine the trend of extant colonies of *C. passerinum* within PNP, we reported the number of colonies that have been extirpated compared to the number of historically known colonies. We tested whether the abundance of remaining colonies of *C. passerinum* increased, decreased, or remained stable between 1970 and 2019, using the number of stalks as a proxy for the number of individuals. We used a mixed effects linear model with "colony" as a random effect and a negative binomial error distribution to account for overdispersion in the count data (Bates *et al.* 2015).

To determine the trend in the percentage of flowering stalks, we calculated the proportion of flowering stalks out of the total number of stalks observed each year of monitoring and determined whether the proportion of flowering stalks was increasing, decreasing, or stable. We used a generalised linear model with a quasi-binomial error distribution to account for overdispersion in the proportion data (Bates *et al.* 2015). We excluded data from 1982 in this analysis because the number of flowering stalks was not recorded (Keddy 1984).

Lastly, we determined if microhabitat condition at colonies (slope, aspect, canopy cover, downed woody debris) contributed to the persistence of colonies. We tested whether slope, aspect, overstorey canopy cover, and downed woody debris were significantly different at colonies that were extant versus those that were extirpated using a two-sample *t*-test, Watson-Williams nonparametric test of homogeneity of means for circular data (Putman *et al.* 2014), or Fisher's exact test for frequencies, respectively. We

considered all analyses significant at α = 0.05. We completed all statistical analyses in R version 3.6.3 (R Core Team 2020).

Results

The total number of *C. passerinum* stalks found within PNP in 2019 was 162, representing only 36.6% of the 1979 population (443 stalks). The total number of stalks decreased significantly from 1979 to 2019 ($\chi^2_{2.3,\,2.8}$ = 66.05, *P* < 0.001; Figure 2).

Nine of the 20 colonies identified in 1983 persisted in 2019. Note that we used the number of colonies in 1983 rather than the number of colonies in 1979 because some colonies were combined beginning in 1982 for the remainder of the monitoring years, and one additional colony was found in 1983. The number of *C. passerinum* stalks at extant colonies has remained stable (β ± SE = 0.004 ± 0.005, *z* = 0.79, *P* = 0.427; Figure 3, Table S1). The proportion of *C. passerinum* stalks flowering has increased by ~1.25% annually (β ± SE = 0.055 ± 0.009, *t* = 5.942, *P* < 0.001; Figure 4, Table S1).

Habitat conditions that were measured in 2019 did not differ among locations of extant and extirpated *C. passerinum* colonies. There were no significant differences in slope ($t_{16.6}$ = −0.433, *P* = 0.67), directional aspect (W_2 = 0.42, *P* = 0.81), canopy cover (Fisher's exact test [two-sided]: *P* = 0.67), or downed woody debris (Fisher's exact test [two-sided]: *P* = 0.21) among locations of *C. passerinum* colonies that survived versus those that have become extirpated (Table 1).

Discussion

The decline in the total number of *C. passerinum* stalks, and the number of extirpated colonies in

FIGURE 2. Total number of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) stalks counted within Pukaskwa National Park, Ontario, Canada between 1979 and 2019. The black line represents a generalised additive model with a negative binomial error distribution of the data and the grey ribbon represents the 95% CI of the predicted model.

this population, is cause for concern, despite a small increase in the number of stalks since 2016 (Table S1: 162, 149, and 173 stalks in 2016, 2017, and 2019, respectively). Although the population trend in extant colonies is stable, a number of the extant colonies possess few stalks (6/9 extant colonies have fewer than 15 stalks each). Extirpation events of colonies decrease genetic diversity (Frankham *et al.* 2002), and the potential of small populations to adapt following chance events or novel conditions is reduced (Willi *et al.* 2006). The number of stalks in a colony is related to the survival of the colony in other species of *Cypripedium* (Shefferson 2006). The average number of stalks over the lifetime of *C. passerinum* colonies that were extirpated (12.9) was lower than in those that survived to 2019 (17.6) in PNP. Decreased population size increases risk of population extirpation in Clustered Lady's-slipper (*Cypripedium fasciculatum* Kellogg ex S. Watson; Kaye *et al.* 2019). As a disjunct population of *C. passerinum*, plants within PNP likely harbour some unique genetic material, thus extirpation could represent a loss of genetic diversity in this species.

The other finding of concern is the increase in the proportion of *C. passerinum* plants flowering within PNP since 1979. Individuals of this species take up to 15 years to flower (Keddy *et al.* 1983), and so the increasing proportion of flowering plants and declining number of stalks suggests that recruitment of new individuals may be limited in this population. A lack of recruitment can contribute to population declines in *Cypripedium* spp. (Nicolè *et al.* 2005). However, *C. passerinum* is not monocarpic nor is the transition between vegetative and flowering status necessarily linear. We did observe back-and-forth transitions between vegetative, flowering, and dormant (subterranean) life stages (e.g., Colony 43 in Table S1), as noted in other species of *Cypripedium* (Shefferson 2006). Thus, this result should be interpreted with caution, but could be clarified by identifying genets and true seedlings in the population.

A likely proximate explanation for the decline in numbers of stalks and ultimately in colonies of *C. passerinum* and the increase in the proportion of flowering plants is that recruitment of *C. passerinum* via sexual propagules (seedlings) is limited. Recruitment occurs via sexual and asexual reproduction in orchids. In 1979, true seedlings, identified by a tapering rhizome <1 cm long, occurred at only 5/20 colonies, and only in early successional habitat (Keddy 1979). We could not collect similar data because we did not dig up colonies. Seed production is an unlikely constraint in this population as self-pollination occurs and a large number of seeds are dispersed; seed germination and survival are more likely constraints (see
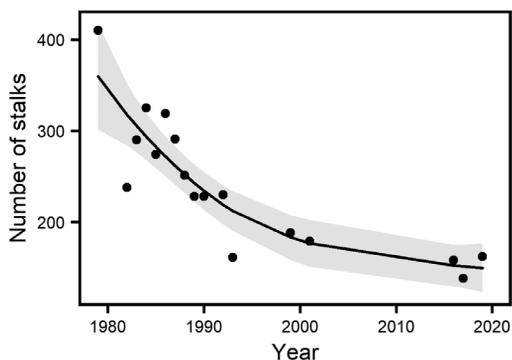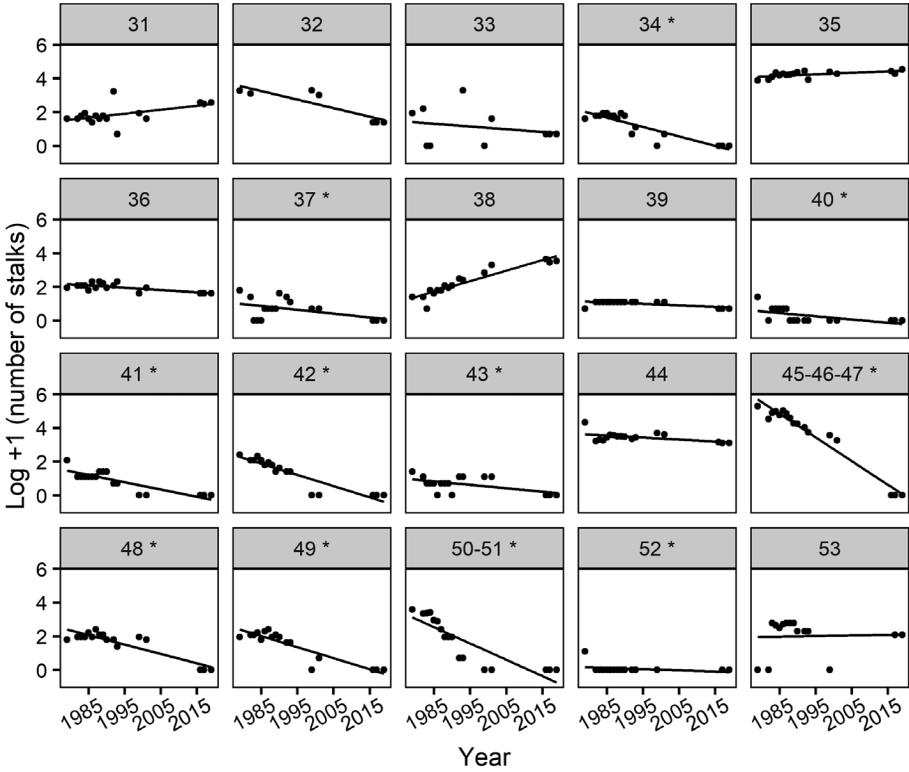
Figure 3. Number of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) stalks (log + 1) counted at each colony within Pukaskwa National Park, Ontario, Canada between 1979 and 2019. Trend lines represent linear models. Colony numbers followed by an asterisk are assumed to be extirpated.

Species biology section). The requirements for seed germination are not well understood in *C. passerinum*, but moisture regime, pH, light levels, and the
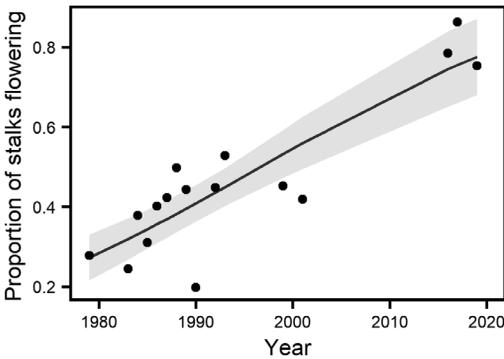
Figure 4. Proportion of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) stalks flowering between 1979 and 2019 in Pukaskwa National Park, Ontario, Canada. The black line represents a generalised linear model with a quasi-binomial error distribution of the data and the grey error ribbon represents the 95% CI of the predicted model.

presence of symbiotic fungi are likely all important factors (see Keddy 1979 for a thorough description). Germinated seeds of *Cypripedium* spp. are unlikely to survive the transition to above-ground stalks. For example, García *et al.* (2010) found that 1–10% of the 5000 seeds/fruit of Lady's Slipper Orchid (*Cypripedium calceolus* L.) were viable and landed in suitable microhabitats, 0.0001–1% of those seeds germinated and survived as protocorms over 3–7 years, and 1–10% of subterranean protocorms produced new stalks; the same pattern may be true for *C. passerinum*. An attempt to propagate *C. passerinum* via seed dispersal was unsuccessful in PNP (Keddy 1984).

Asexual reproduction is an important mechanism of recruitment in orchids generally (Shefferson 2006) and of *C. passerinum* within PNP (Keddy 1979). Clonal offspring increase resource acquisition from a heterogeneous environment and can reduce mortality risk to the individual (Shefferson 2006). Asexual reproduction likely occurs more rapidly than sexual reproduction in *C. passerinum* and may improve survival of genetic individuals (Keddy 1979). Conditions

TABLE 1. Descriptive statistics for slope (°), directional aspect (°), canopy cover (%), and downed woody debris coverage (%) at locations of extant and extirpated colonies of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) in Pukaskwa National Park, Ontario, Canada in 2019.

	Summary statistic	Extant colonies ($n = 9$)	Extirpated colonies ($n = 10$)
Slope (°)	Mean ± SD	24 ± 12.86	21.5 ± 12.20
Aspect (°)	Circular median ± circular deviation	215 ± 1.34	48.5 ± 1.43
Canopy cover (%)*	Mode (*ns*†)	0–24 (5)	0–24 (6)
Downed woody debris (%)*	Mode (*ns*†)	0–24 (7)	0–4 (10)

*Canopy cover and downed woody debris were assessed using these categories: 0–24%, 25–49%, 50–74%, and 75–100%.
†The number of sites that scored in the category of the mode (*ns*) out of the total sample is represented in brackets.

for vegetative reproduction in *C. passerinum* are not well understood, but occur in both early and late stages of dune succession to forest (Keddy 1979).

Many orchids have specific habitat requirements, and lack of favourable habitat conditions may be limiting persistence and recruitment of *C. passerinum* in PNP. Keddy (1979) found maximum soil temperature, presence of sand, presence of canopy, and soil moisture were statistically different between sites with *C. passerinum* present and random locations where it was absent in 1979. This suggests that habitat conditions in space (i.e., site selection) and time (i.e., variation in precipitation, temperature) are important factors for survival and reproduction (Keddy 1979; Keddy *et al.* 1983).

Habitat requirements of *C. passerinum* may also vary during the life of an individual (Keddy *et al.* 1983). Seedlings in 1979 were found in early successional habitat at PNP, including White Spruce (*Picea glauca* (Moench) Voss) canopy with thick needle cover on the ground, Common Juniper (*Juniperus communis* L.) with needle cover, open dunes, and sand/litter including needles with no canopy (Keddy 1979; Keddy *et al.* 1983), while no seedlings were found at colonies where sphagnum moss (*Sphagnum* sp.) co-occurred despite abundant seed production (Keddy 1979; Keddy *et al.* 1983). This suggests that late-successional habitat (i.e., where canopy cover is sufficient for sphagnum moss to establish) is not suitable for seed germination but rather asexual reproduction alone and presents an increased risk of eventual extirpation (Keddy 1979; Keddy *et al.* 1983). Notably, the largest colony (45-46-47) of *C. passerinum* within PNP that became extirpated was located in a mossy area. Colonies 35 and 38, which have both increased in the number of total stalks since 1979 (Figure 3), are also located in sphagnum moss, suggesting that clonal reproduction is solely responsible for the stability in extant colonies of *C. passerinum* in PNP.

We did not find a difference in habitat conditions we measured (i.e., slope, aspect, canopy cover, and downed woody debris) in locations of colonies that

survived versus those that were extirpated by 2019. However, sample size for this analysis was small ($n = 19$) and current conditions may not coincide with the conditions under which colonies disappeared. Moreover, we did not measure other microsite conditions that may influence survival and recruitment (e.g., Keddy 1979), such as soil pH, temperature, and moisture.

Habitat changes may be occurring in PNP's population of *C. passerinum* for several reasons. First, long-term climatic trends for the region include an increase in average air temperatures (Parks Canada Agency 2017), an increase in summer surface water temperature of Lake Superior (Austin and Colman 2008; Noël *et al.* 2019), and a corresponding decline in ice cover (Austin and Colman 2008; Wang *et al.* 2017; Parsons and Patterson 2020). Climate influences local habitat characteristics, such as soil temperature, moisture, and chemical composition, that affect vegetation growth. Climatic changes may also influence the persistence of species symbiotic with *C. passerinum*, such as the fungal mycorrhizal species necessary for seed germination (Keddy *et al.* 1983). The population of *C. passerinum* near the Pic River occurs as a southeastern disjunct of its distribution (Keddy 1979), meaning that warming temperatures may exceed what is suitable for this northerly species.

The second potential cause of habitat change is stabilization of the dune ecosystem where this population occurs. *Cypripedium passerinum* generally inhabits riverbanks and lakeshores—areas that are unstable but always present (Luer 1975; Keddy *et al.* 1983), which suggests this plant relies on some degree of disturbance. Dune stabilization results from a reduction in wind exposure, vegetation establishment, and, ultimately, succession to forest (Noël *et al.* 2019). In PNP, dune stabilization may have occurred due to driftwood accumulation (43–78% coverage) on beaches within the active cove dune system since 1978 (Noël *et al.* 2019) and the establishment of roads, campsites, and day-use trails in 1983. Succession from dunes to forest has occurred, as open sand

and low-lying vegetation has been replaced by mature forest, according to analysis of aerial images from 1937 to 2016 (Noël *et al.* 2019). The slow change of *C. passerinum* habitat due to forest succession was identified in monitoring reports (Keddy 1984; Vien and Mosquin 1986; Vien 1990; Reside 1993) and could be linked to lack of recruitment in the population.

Trampling is another potential factor that may impact the persistence of the *C. passerinum* population in PNP, and is identified as a threat to this species by the IUCN (Rankou 2014). The *C. passerinum* population in PNP is found in Zone I—Special Preservation, the highest protective level within Parks Canada Agency's zoning system (Parks Canada Agency 2015); the area is restricted to visitors unless accompanied by a PNP chaperone. The colonies are fenced and signed, and are rarely accessed by the public. However, there are 13 records of this population by 10 different people posted on iNaturalist (as of 6 January 2022; https://inaturalist.ca), suggesting that this population is visited by the public without knowledge of park management, even though the geolocation of the plants is obscured. Additionally, some colonies are within 5 m of a historical access trail used by PNP staff. Use of this trail ceased in 2017, but could have contributed to extirpation of some colonies. To reduce the impact of monitoring, staff wear soft-soled shoes to complete their monitoring work (Promaine and Nabigon 1997).

To better inform management and reverse this population trend, more research on the ecology of *C. passerinum* is necessary. Research should aim to define the habitat requirements of *C. passerinum*, including asexual reproduction and seed germination requirements, symbiotic fungi, and survivorship in different habitats (Keddy *et al.* 1983). Marking unique individuals could provide information on life history, recruitment, and dormancy. Active management strategies for restoration such as seed propagation experiments could be performed to further our understanding of germination, survival, and growth of sexual propagules and increase population size. *In vitro* reproduction could be a short-term solution to supplement population recruitment until habitat and reproductive requirements are better understood, as has been completed successfully for *C. passerinum* in the past (Curtis 1936).

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Writing – Original Draft: C.C.I.; Writing – Review & Editing: L.D.P.; Investigation: C.C.I and L.D.P.; Formal Analysis: C.C.I. and L.D.P.

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Supplementary Material:

Table S1. Number of flowering and total stalks of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) within colonies in Pukaskwa National Park, Ontario, Canada monitored between 1979 and 2019.

Note

Gimme shelter: anthropogenic structures as resting sites for American Marten (*Martes americana*)

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Abstract
Several species of martens (*Martes* spp.) are reported to use buildings as resting or den sites. However, such behaviour has not been attributed to American Marten (*Martes americana*). We report American Marten using occupied buildings and evidence of suspected use of an abandoned cabin, as resting sites in southern Yukon, Canada. These observations further highlight the behavioural flexibility of North American species of *Martes* with regard to using novel structures as resting sites.

Key words: Commensal; human–wildlife interactions; resting site; synurbic; urbanization; American Marten; *Martes americana*

Martens (*Martes* spp.) use resting sites daily between bouts of activity (Buskirk 1984; Brainerd *et al.* 1995; Birks *et al.* 2005; Robitaille *et al.* 2020). Suitable resting sites are a critical resource for martens, as they provide protection from predators and inclement weather, as well as thermoregulatory benefits and close access to prey (Buskirk 1984; Zalewski 1997; Larroque *et al.* 2015, 2017; Delheimer *et al.* 2018). Martens use various structures as resting sites: most are associated with live or dead trees, either standing or fallen, but also frequently include piles of rocks (Buskirk 1984; Spencer 1987; Buskirk *et al.* 1989; Bull and Heater 2000; Birks *et al.* 2005; Larroque *et al.* 2015). Several species of martens also use buildings as resting sites. In Europe, for example, Stone Marten (*Martes foina*) inhabit buildings almost exclusively, particularly barns (Rondinini and Boitani 2002; Larroque *et al.* 2015; Czernik *et al.* 2016). Pine Marten (*Martes martes*) in Europe also use buildings, but more occasionally and particularly where natural resting sites may be limited (Birks *et al.* 2005).

In western North America, Pacific Marten (*Martes caurina*) has been reported to use buildings as resting or denning sites, albeit rarely. Specifically, radio-tracked individuals have used three primitive cabins in Oregon (Holyan *et al.* 1998), two in California (Spencer 1987), and two others in Montana

(Ruggerio *et al.* 1998). Several other incidental observations also exist, including those listed by Holyan *et al.* (1998) and two using an equipment shed and the crawl space of a house in New Mexico (J. Stuart pers. comm. 3 August 2015). In one observation, a Pacific Marten occupied the accommodations building of a busy tourist lodge outside Grand Teton National Park, Wyoming (E. Beever pers. comm. 4 August 2015). For more than a decade, more than one marten was reported to use the historic Cloud Cap Inn in Mount Hood National Forest, Oregon, as a resting or denning site (L. Ruedas pers. comm. 4 August 2015). Common among these reports is that the buildings occupied by Pacific Marten were in rural or remote areas, where few other buildings were available and natural resting sites were likely not limiting. However, in parts of California, natural cavities suitable as resting sites may be limiting (Delheimer *et al.* 2019), and artificial housing structures have been used successfully by Pacific Marten (Delheimer *et al.* 2018). Regardless, although use of anthropogenic structures by Pacific Martens has been observed, it appears to be rare.

Until recently, the resting sites noted above for Pacific Marten were attributed to American Marten (*Martes americana*) in the literature (i.e., Spencer 1987; Holyan *et al.* 1998; Ruggerio *et al.* 1998). Pacific Marten and American Marten are now con-

sidered separate species that differ genetically, morphologically, and by distribution (e.g., Lucid *et al.* 2020). All of the known instances of martens occupying buildings in North America can be attributed to Pacific Marten based on their distribution. Here, we report observations of American Marten occupying buildings in the Yukon.

For three months beginning in August 2015, two American Marten were reported by a homeowner to be entering a garage beside an occupied house (Figure 1). The martens had been resting in the fiberglass insulation where the walls met the roof (Figure 1). Martens had not previously been observed using the garage. On occasion, they were also heard chasing one another inside the roof of the occupied house. A year later, one marten also used the buildings as a resting site for about a week, but none have since then. The building used by martens was about 18 km north of Whitehorse, Yukon, Canada. Housing density there was low and the area was densely forested, with Lodgepole Pine (*Pinus contorta* Douglas ex Loudon), White Spruce (*Picea glauca* (Moench) Voss), and Trembling Aspen (*Populus tremuloides* Michaux) being common trees. Most of the trees were young, as much of the area burned in a severe forest fire in 1958. It is not known whether trees or downed logs suitable as resting sites were limited in the local area, but they may have been given the younger age class of much of the forest.

In another confirmed report, an American Marten was observed living in the roof of an unoccupied house during late March 2005 when the homeowners returned from vacation. The marten and her kits lived in the roof for about 10 days after the house was again occupied, but then relocated. They were observed repeatedly entering the roof during that time and a number of times on the property after they left the house. The rural property was about 14 km south of Whitehorse and surrounded by mature White Spruce forest. In both this instance, and that in 2015, martens were heard by property owners in the roofs of their homes.

Finally, on 8 September 2004, we visited an isolated and abandoned log cabin about 55 km northwest of Teslin, Yukon, to monitor a population of Little Brown Bat (*Myotis lucifugus*; Jung and Slough 2005). We observed four or five dismembered tails of Red Squirrel (*Tamiasciurus hudsonicus*) as well as numerous Spruce Grouse (*Falcopennis canadensis*) feathers in the cabin. Both species are prey of martens in the Yukon (Slough *et al.* 1989). Holyan *et al.* (1998) found similar prey remains in a cabin in Oregon that was used by Pacific Marten. We believe that our observations also indicated that an American Marten was using the cabin as a resting site. However, we could not confirm that a marten resided in the cabin.

FIGURE 1. Photographs of an American Marten (*Martes americana*) using a garage as a resting site near Whitehorse, Yukon, Canada. Photos: Gordon Settle.

It is not known why martens occasionally use buildings. They may be attracted to buildings that harbour other human commensals, such as small rodents, although some have disputed this (Holyan *et al.* 1998). In the case of the abandoned log cabin in the Yukon, the smell and noise of a maternity colony of Little Brown Bats may have been an attractant. A main driver for some species to use buildings rather than natural roosts is that they provide energy benefits (e.g., Lausen and Barclay 2006; Larroque *et al.* 2017) or protection from predators, such as Red Fox (*Vulpes vulpes*; Birks *et al.* 2005). Like other mustelids, martens are long and lean with limited fat reserves (Buskirk and Harlow 1989; Robitaille and Cobb 2003), and their body shape comes with high energy costs (Brown and Lasiewski 1972). Even though some of our observations are from August and September, nightly minimum temperatures are frequently <5°C in southern Yukon at that time of year. Thus, American Marten may have been using buildings largely for their thermoregulatory benefits.

Over the years, we have heard of a couple of other instances of American Marten living in buildings in the Whitehorse area, particularly during winter; however, we did not recognize the significance of these observations at the time or follow up with property owners. The frequency at which American Marten use anthropogenic structures as rest sites is unknown, but may be more common than reported. The implications of martens living commensally with humans are also unknown but may include human–wildlife conflicts related to property damage or transmission of parasites or pathogens to people or pets. Moreover, use of buildings may be an ecological trap for martens that may be killed by dogs or because of conflicts with humans. In southwestern Yukon, martens persist at low densities that have been augmented through translocations (Slough 1989). In recognition, the region has been designated as a marten conservation area to protect American Marten, with strict quotas for fur trappers (Jung and Slough 2011); however, martens have apparently increased in the region since the transplants in the 1980s, likely because of a natural increase in older forest.

In conclusion, the value of our confirmed and suspected observations of American Marten using buildings as resting sites is that these are apparently the first documented for the species. These observations demonstrate the flexibility that some individuals may have in selecting suitable resting sites, similar to that of other species of *Martes*.

Acknowledgements

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Continuing expansion of Narrow-leaved Cattail (*Typha angustifolia*) and decline of a provincially rare fen in the Holland Marsh, Ontario

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Abstract
At the time of European settlement, an extensive graminoid wetland existed at the confluence of the East and West Holland Rivers at the southern end of Lake Simcoe, Ontario. However, by 1925, clearing and draining of the marsh for specialty agriculture (i.e., market gardens) had begun and, by the 1940s, ~46% of the wetland had been cleared and another 13% was lost before 2016. Concurrent with marsh conversion has been an increase in Narrow-leaved Cattail (*Typha angustifolia*) in the remnant wetland. This study documents the change in the Holland Marsh wetland by delineating boundaries between marsh, fen, and shrub communities on aerial photographs taken at ~10-year intervals between 1946 and 2015 and documenting vegetation change along transects running perpendicular to tributaries bisecting the wetland. The extent of fen habitat within the Holland Marsh has been decreasing since 1946 at an average rate of 0.24 ha/year because of increases in both shrub and marsh (i.e., *T. angustifolia*) communities. *Typha angustifolia* expansion has been predominantly from along the margins of the Holland River where soil phosphorus concentration is significantly higher than in the core of the fen. Beyond 30 m from the river, vegetation dominance shifts from *T. angustifolia* to sedges (Cyperaceae). Managing phosphorus loading from upstream land uses will be of critical importance in protecting this habitat, which is rare in southern Ontario.

Key words: Fen eutrophication; Lake Simcoe; *Typha*; phosphorus; cattail invasion; fen decline; *Carex*; photointerpretation

Introduction

It has been estimated that over half of the total area of wetland in North America has been lost as a result of European settlement (Davidson 2014), with some of the greatest pressures in Canada occurring in southern Ontario (NWWG 1988). For example, at the time of European settlement, an extensive graminoid wetland existed at the confluence of the East and West Holland Rivers at the southern end of Lake Simcoe. This wetland was described variously as a "quaking bog, a typical sphagnum area, which quivers and shakes under people walking upon it" (Saunders 1947: 169); "an open bog, which quakes as one passes over it" (Devitt 1939: 239); or composed of "almost pure carpets of Canada bluejoint [*Calamagrostis canadensis*] … extending for thousands of acres" (Mayall 1938: 18).

However, by 1925, draining and clearing of the marsh for specialty agriculture (i.e., market garden crops) had begun and, by the 1940s, ~4600 ha (or 46% of the wetland) had been cleared (Sendel 1992), with an additional 13% lost up to 2016 (Kissel and Choi 2018). Despite this extensive clearing, evaluation of the Holland Marsh under the Ontario Wetland Evaluation System in 1984 mapped 272 ha of fen communities (Power *et al*. 1984), making it one of the largest fens in southern Ontario (OMNRF 2013), where fens are considered provincially rare (Bakowsky 1996). Over the years, a number of rare species have been recorded from this fen, including Eastern Prairie Fringed-orchid (*Platanthera lecuophaea* (Nuttall) Lindley), King Rail (*Rallus elegans*), Yellow Rail (*Coturnicops noveboracensis*), Black Tern (*Chlidonias niger*), and numerous regionally rare plants such as Creeping Sedge (*Carex chordorrhiza* L.), Sartwell's Sedge (*Carex sartwellii* Dewey), Slender Cotton-grass (*Eriophorum gracile* W.D.J. Koch ex A. Roth), and Poison Sumac (*Toxicodendron vernix* (L) Kuntze; MTO 1984; Power *et al*. 1984; Cadman *et al*. 2007).

The invasion of cattails (*Typha* spp.) into graminoid wetlands has been observed throughout North America (e.g., Day *et al*. 1988; Wu *et al*. 1997; Woo and Zedler 2002; Wilcox *et al*. 2008; Tuchman *et al*.

2009; Duval *et al*. 2012; Bansal *et al*. 2019). Three species of cattail are known from the Great Lakes basin: Broad-leaved Cattail (*Typha latifola* L.), which is native to the area; Narrow-leaved Cattail (*Typha angustfolia* L.), which may be a European introduction or a native species that has greatly increased in range; and their hybrid, Blue Cattail (*Typha ×glauca* Godron). Despite uncertainty about the North American origin of *T. angustifolia*, all three species have increased in abundance in the Great Lakes basin since the time of European settlement (Grace and Harrison 1986; Shih and Finkelstein 2008). Their proliferation has been associated with a competitive advantage provided by changes in hydrology (Wilcox *et al*. 1984, 2008; Day *et al*. 1988), sedimentation (Werner and Zedler 2002), and nutrient enrichment (Auclair *et al*. 1976; Wu *et al*. 1997; Duval *et al*. 2012). Nutrient enrichment in the East and West Holland Rivers has long been a concern for watershed managers; concurrent with marsh conversion has been an increase in agriculture and urbanization in these watersheds, which has been associated with increased phosphorus loadings in the East Holland River and Lake Simcoe (Nicholls and MacCrimmon 1975; Johnson and Nicholls 1989; Evans *et al*. 1996; North *et al*. 2013).

The objectives of my study were to determine whether Narrow-leaved Cattail has expanded in the Holland Marsh since agricultural conversion and to assess whether the limits of *T. angustifolia* are associated with abiotic conditions within the marsh.

Methods

Study area and interpretation of aerial photos

Holland Marsh is a 3247-ha wetland complex at the south end of Lake Simcoe at the confluence of the East and West Holland Rivers in York Region and Simcoe County, Ontario (44.19°N, 79.52°W). The two wetland blocks within the Holland Marsh Provincial Wildlife Area selected for this study (104 and 63 ha in size) are separated from one another by a small tributary of the Holland River (Figure 1).

In July 2016, boundaries between vegetation communities were mapped in the field using a handheld global positioning system (GPS) unit (Garmin eTrex 20, Olathe, Kansas, USA) and a set of printed colour aerial photographs from 2015. Communities were defined as marsh where *T. angustifolia* occurred at ≥25% cover, as shrub thicket when shrubs occurred at ≥25% cover (following Lee *et al*. 1998), and graminoid fen otherwise.

These field-mapped boundaries were then digitized on aerial photographs taken in 2015 at a scale of 1:2000 using a minimum mapping unit of 0.01 ha (~10 m × 10 m) in ArcGIS 10.0 (ESRI, Redlands, California, USA). Boundaries between these commu-

nities were then mapped on a time series of air photos from the same area taken at approximately decadal intervals (i.e., 1946, 1969, 1978, 1988, 1999, and 2005) each at a scale of 1:2000 and a minimum mapping unit of 0.01 ha (Table 1). These boundaries were mapped based on observed differences in reflectance pattern between fen, marsh, and thicket communities in the 2015 aerial photographs compared with such differences in each successive set of photos in the time series. Because of variations in resolution in the air photos, vegetation boundaries may vary somewhat over the period of record. To minimize the effects of changing photo resolution, a consistent scale (i.e., 1:2000) was used in digitization. After the delineation of all boundaries, the area of each vegetation community was calculated in ArcMap (ESRI).

Vegetation and soil sampling

Plant community composition in the fen and marsh communities was quantified in July and August 2016. Three sets of transects were established: two in the larger (north) block and one in the southern block. Each set was composed of three transects, randomly located along the tributaries, which formed the north and south boundaries of the wetland blocks, and extending up to 250 m long, oriented perpendicular to the boundary between the fen and marsh communities. Five 1-m^2 quadrats were randomly located along each of these transects. The total number of stems of each plant species was counted in a 0.1 m × 0.1 m subsample from the corner of each quadrat. Plant species were identified using Voss and Reznicek (2012). Although no formal vouchers were deposited in a herbarium, a few specimens are in the personal collection of B.A.T.

Soil cores (~20 cm diameter and 10 cm deep) were collected from the centre of each quadrat as determined using a GPS unit. A subsample of soil from each core was weighed and dried at 80°C for 24 h before reweighing to determine soil moisture. Organic matter content of the soil was estimated by combusting the sample for 3 h at 500°C and reweighing to determine the percentage of the sample lost to ignition. Samples were analysed for concentrations of total phosphorus (P), magnesium (Mg), and potassium (K) by the Agriculture and Food Laboratory at the University of Guelph. Briefly, phosphorus was extracted from the samples using a 0.5 mol/L solution of sodium bicarbonate, and the concentration of phosphorus in the extract was determined using a colorimeter. Similarly, magnesium and potassium were extracted from the samples using a 1.0 mol/L solution of ammonium acetate, and their concentration in the extract determined using an inductively coupled plasma–optical emission spectrophotometer.
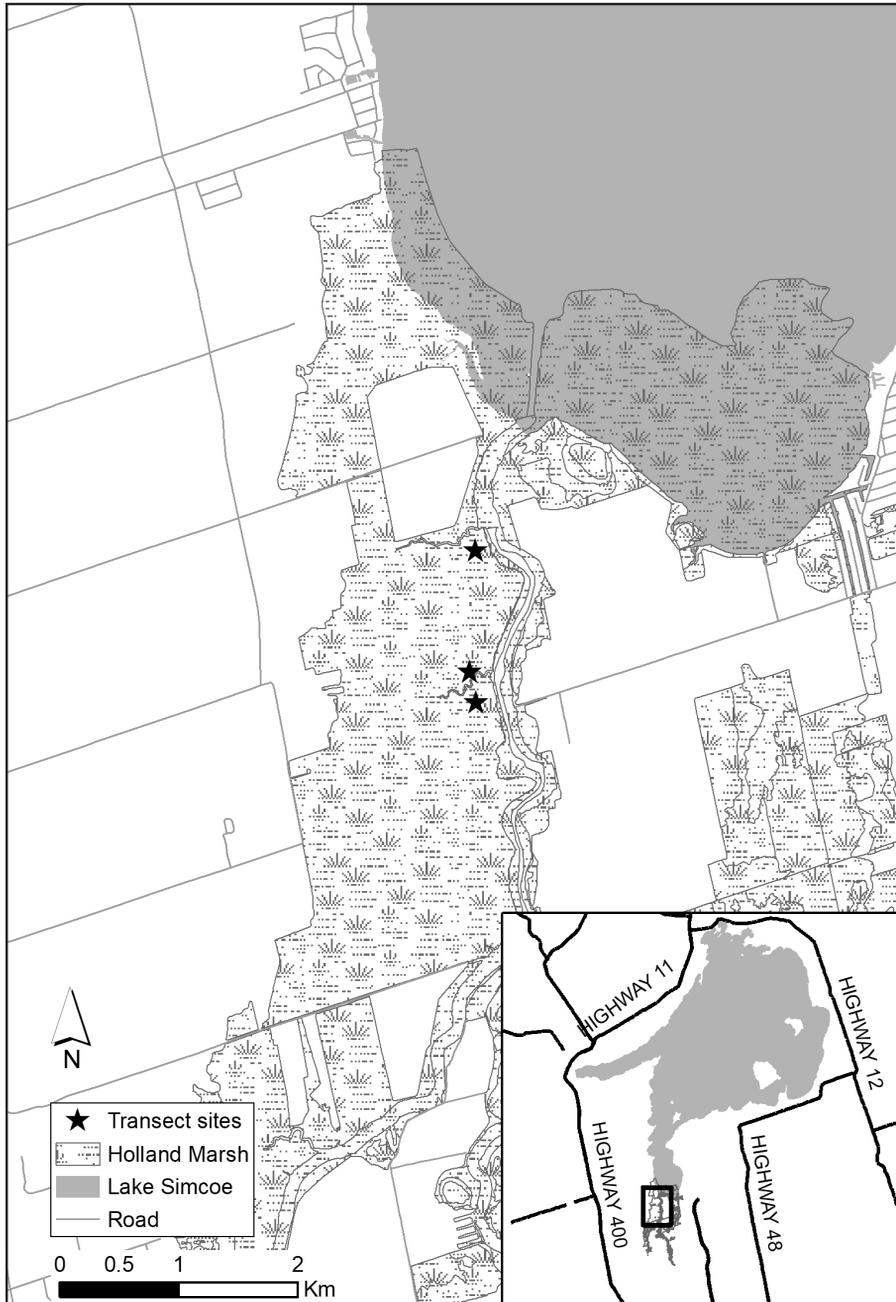
FIGURE 1. Location of transects within the Holland Marsh, with inset showing location relative to Lake Simcoe, Ontario.

Statistical analyses

Change in extent of fen and non-fen communities in the Holland Marsh wetland complex since 1946 was assessed by regressing the total area mapped as fen community against year in which the air photos were taken. The density of stems of *T. angustifolia*

and members of the Cyperaceae (including *Carex* spp., *Eleocharis* spp., and *Eriophorum* spp.) was averaged across the four subsamples within each quadrat. The influence of abiotic conditions in the wetland (i.e., distance from the river, soil moisture, organic matter, and soil concentrations of P, Mg, and K) on

Table 1. Aerial photographs used in delineating plant communities in the Holland Marsh fen, Ontario.

Year	Photo source	Photo type	Resolution*, cm
1946	Ontario Department of Lands and Forests	Black and white	130
1969	Ontario Department of Lands and Forests	Black and white	130
1978	Ontario Ministry of Natural Resources	Black and white	130
1988	Northway Remote Sensing Limited	Natural colour	130
1999	Triathlon Incorporated	Natural colour	50
2005	First Base Solutions	Natural colour	20
2015	First Base Solutions	Natural colour	15

*Refers to the size of the pixel in the digital image (i.e., the 1946 air photos were of lower resolution than the 2015, as each pixel in the 1946 image covered an area 130 cm in size, as opposed to those more current images which showed features as small as 15 cm). Resolution is a fundamental challenge in comparing current with historical air photos.

their abundance was assessed using linear regression. Similarly, relations between distance from the river and these abiotic conditions were also assessed using linear regression.

Before analysis, all dependent variables were tested for normality, using the Shapiro-Wilk method (Shapiro and Wilk 1965), and any with a significantly ($P < 0.05$) non-normal distribution were transformed. Stem density was log-transformed and soil concentrations of P, Mg, and K were square root-transformed. All analyses were done using R version 3.6.3 (R Core Team 2020).

Results

Marsh communities in the study wetlands were dominated by Narrow-leaved Cattail, but also included species, such as Purple Loosestrife (*Lythrum salicaria* L.; the only non-native), Leatherleaf (*Chamaedaphne calyculata* (L.) Moench), Marsh Cinquefoil (*Comarum palustre* L.), Northern Aster (*Symphyotrichum boreale* (Torrey & A. Gray) A. Love & D. Love), Marsh Fern (*Thelypteris palustris* Schott), Boneset (*Eupatorium perfoliatum* L.), and Spotted Joe Pye-weed (*Eutrochium maculatum* (L.) E.E. Lamont). Fen communities in the study wetlands were of two kinds: one dominated by *Carex* (including Slender Sedge [*Carex lasiocarpa* Ehrhart], Lesser Panicled Sedge [*Carex diandra* Schrank], and Water Sedge [*Carex aquatilis* Wahlenberg]), with *C. palustre*, Elliptic Spike-rush (*Eleocharis elliptica* Kunth), Marsh St. John's Wort (*Hypericum fraseri* (Spach) Steudel), *S. boreale*, and *T. palustris*; or one dominated by *E. gracile* with *C. palustre*, Water Horsetail (*Equisetum fluviatile* L.), *T. palustris*, and Sweet Gale (*Myrica gale* L.) in scattered clumps.

The extent of fen habitat in the Holland Marsh has been decreasing since 1946 at a relatively constant rate of ~0.24 ha/year ($F_{1,5} = 130.2$, $P < 0.001$; Figure 2). Between 1969 and 1988, much of that conversion was associated with the expansion of shrub communities into the fen (although shrub expansion into

the marsh was greater). Shrub expansion into the fen has been non-existent since 1988 (Figures 1, 2). Much of the expansion of *T. angustifolia* into the fen has occurred along the margin of the Holland River, as the *T. angustifolia* margin along the river and its tributaries has gradually increased in width over time, and in the fen in the south block of the wetland (which was encircled by marsh; Figure 3).

In 2016, *T. angustifolia* was significantly ($F_{1,42} = 34.92$, $P < 0.001$) less abundant beyond ~45 m from the river (Figure 4a). Beyond ~30 m from the river, members of the Cyperaceae (i.e., *Carex* spp. and *Eriophorum* spp.) were significantly more abundant ($F_{1,42} = 15.17$, $P < 0.001$; Figure 4b). Aside from that small margin of overlap between *Typha* and Cyperaceae communities, these two taxa did not tend to co-occur within the same quadrat; rather, they were significantly ($F_{1,42} = 12.64$, $P < 0.001$; Figure 5c) negatively associated.
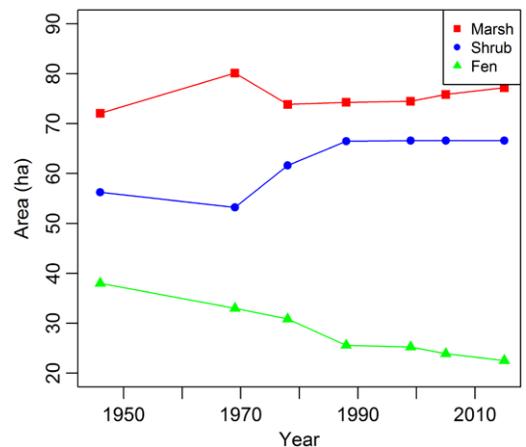
Figure 2. Change in extent of wetland communities in the Holland Marsh, Ontario, as interpreted from aerial photographs between 1946 and 2015. Fen area has decreased at an average rate of 0.24 ha/year ($F_{1,5} = 130.2$, $P < 0.001$).
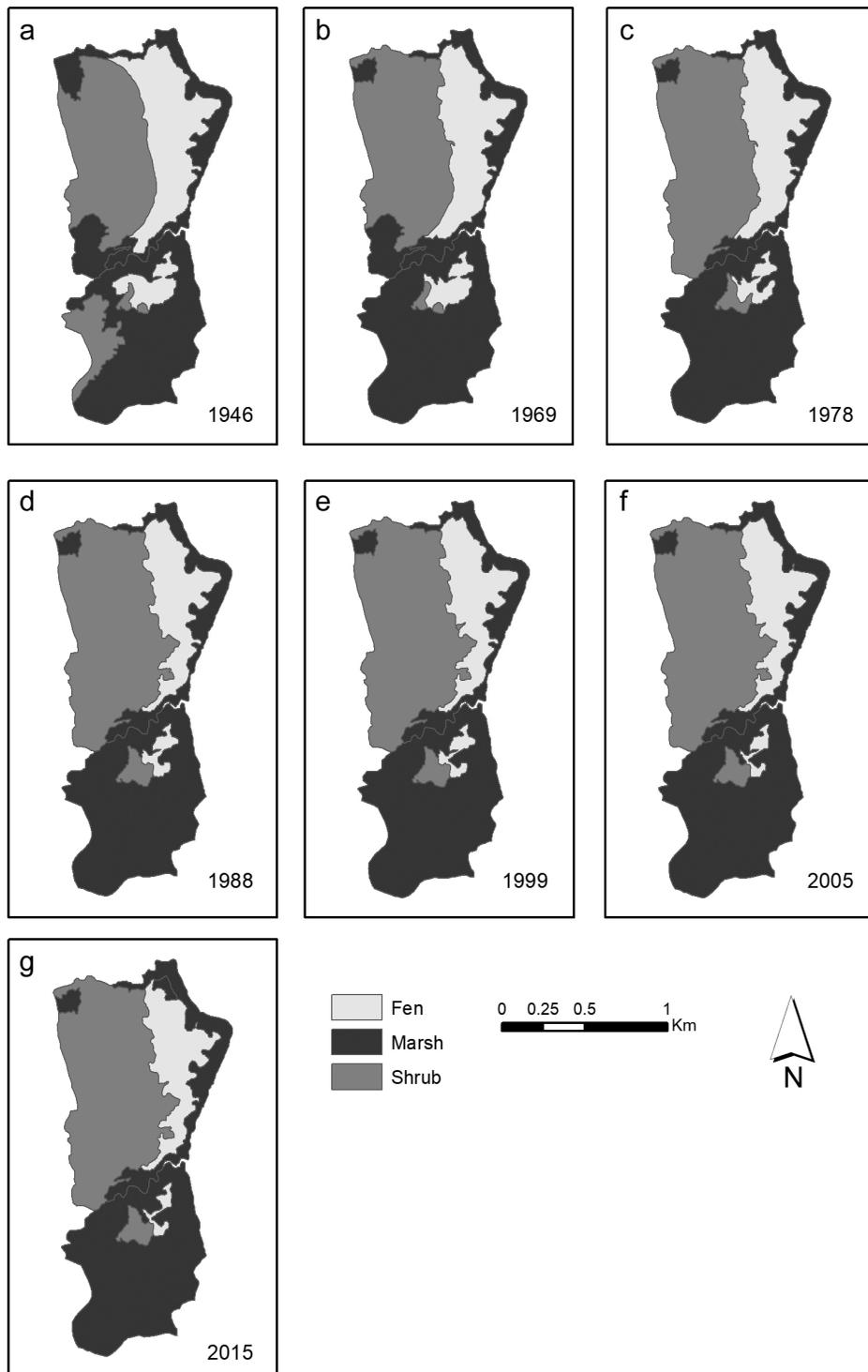
Figure 3. Change in distribution of wetland communities in the Holland Marsh, Ontario, as interpreted from a time series of aerial photographs taken between 1946 and 2015. Community boundaries delineated at a scale of 1:2000, with minimum mapping unit of 0.01 ha.
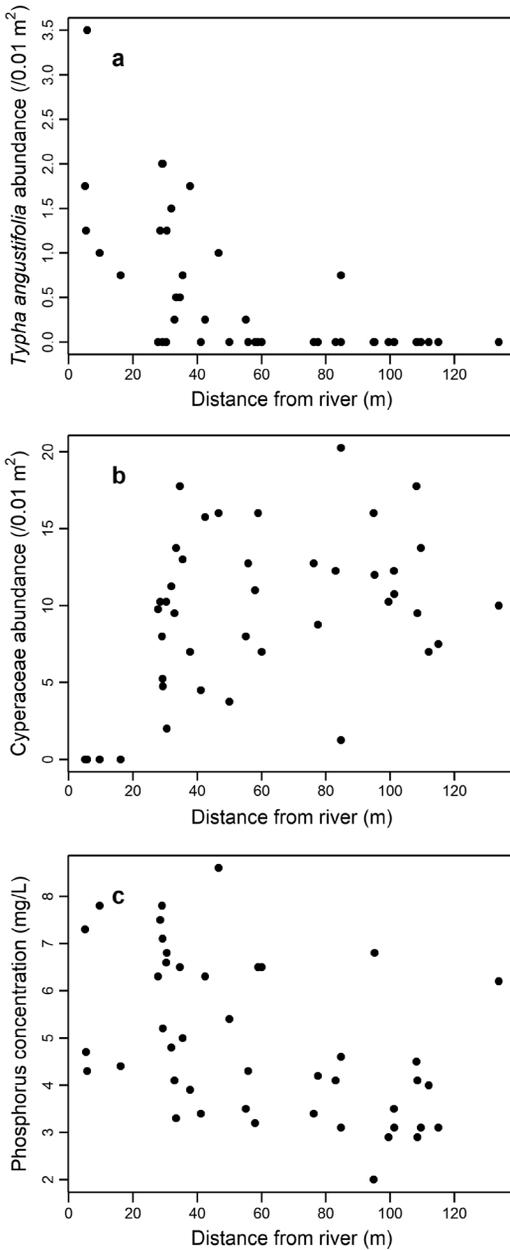
FIGURE 4. Influence of distance from watercourse on the abundance of a. Narrow-leaved Cattail (*Typha angustifolia*; $F_{1,42} = 44.61$, $P < 0.001$), b. members of the Cyperaceae ($F_{1,42} = 26.5$, $P < 0.001$), and c. soil phosphorus concentration ($F_{1,42} = 13.13$, $P < 0.001$).

FIGURE 5. Relation between soil phosphorus concentration in the Holland Marsh wetland complex and a. abundance of Narrow-leaved Cattail (*Typha angustifolia*; $F_{1,42} = 6.62$, $P = 0.014$), b. abundance of Cyperaceae ($F_{1,42} = 0.94$, $P = 0.34$). c. Influence of *T. angustifolia* on Cyperaceae abundance ($F_{1,42} = 12.64$, $P < 0.001$).

Phosphorus concentration in the soil decreased in a linear fashion with distance from the river ($F_{1,42} = 13.67$, $P < 0.001$; Figure 4c). Soil moisture, soil organic matter, and the concentration of Mg and K

in the soil were not significantly associated with distance from the river ($P > 0.05$ in all cases; data not shown). Soil P concentration was positively associated with *T. angustifolia* abundance ($F_{1,42} = 6.62$, $P =$

0.014; Figure 5a), with *T. angustifolia* not occurring below a soil phosphorus concentration of 3.3 mg/L. The abundance of Cyperaceae, however, did not respond significantly to soil P concentration ($F_{1,42} =$ 0.94, $P = 0.34$; Figure 5b).

Discussion

At the time of European settlement, *Typha* spp. were a minor component of the flora of marshes in the Great Lakes basin; however, they have been increasing in dominance since that time (Shih and Finkelstein 2008; Wilcox *et al*. 2008; Rippke *et al*. 2010; Wilcox and Bateman 2018; Smith *et al*. 2021). In the Holland Marsh, *T. angustifolia* has been expanding since the 1940s (Figure 2). Over the same period, much of the Holland Marsh wetland has been converted from wetland to farmland (Sendel 1992; Kissel and Choi 2018), and urbanization in its watershed has increased by a factor of four (Eimers *et al*. 2005).

The expansion of species of *Typha* into sedge-dominated fens has been documented elsewhere (Auclair *et al*. 1976; Wilcox *et al*. 1984; Rutchey and Vilchek 1999; Duval *et al*. 2012), with rates ranging from 35 ha/year (Smith 1967) to as much as 306.1 ha/year or 833 ha/year into Sawgrass (*Cladium jamaicense* Crantz)-dominated communities in the Everglades (Wu *et al*. 1997; Rutchey and Vilchek 1999). In the Holland Marsh wetland, *Typha* expansion into the sedge fen has largely been along the Holland River and its tributaries (Figure 3). Studies elsewhere have found similar patterns, with *Typha* invasion into sedge communities associated with an increasing dominance of *Typha* near watercourses and other flow structures, which spread further inland as an invading front (Koch and Reddy 1992; Wu *et al*. 1997; Rutchey and Vilchek 1999). The expansion of *Typha* into *Cladium*-dominated communities in the Everglades has been associated with phosphorus loads in surface waters enriching riparian soils (Koch and Reddy 1992; Newman *et al*. 1998). Similarly, P loads are high in the Holland River, as a result of agricultural and urban influences with its watershed (Johnson and Nicholls 1989; Evans *et al*. 1996). Although much effort has been expended to reduce these loads, a clear relation exists between P concentration in soils in this wetland and distance from the river (Figure 4c).

Within the invading front of *Typha* and the transition zone to sedge fen in the Holland Marsh, soil P concentration is associated with an increased abundance of *T. angustifolia* (Figure 5a), but has no statistically significant relation to the abundance of Cyperaceae (Figure 5b). Fertilization studies have similarly found that the addition of P to natural wetlands or mesocosms increases the abundance of *Typha* spp., but does not tend to influence the abundance of native graminoids including *Carex* (Wetzel and van der Valk 1998; Lorenzen *et al*. 2001; Woo and Zedler 2002). The addition of P fertilizer led to increased leaf and shoot biomass in *Typha* (Wetzel and van der Valk 1998; Miao *et al*. 2000; Woo and Zedler 2002; Steinbachová-Vojtíšková *et al*. 2006), which can allow *Typha* to create more leaf litter in P-enriched wetlands, which in turns tends to decrease the abundance and germination rate of native graminoids (Day *et al*. 1988; Tuchman *et al*. 2009; Larkin *et al*. 2012).

Some have suggested that a threshold may exist in the relation between P availability and *Typha* expansion. For example, Wu *et al*. (1997) found that the probability of cattail invasion into *Cladium*-dominated communities rapidly accelerated when soil P concentration exceeded 400 mg/kg. Above 650 mg/kg, however, the probability of invasion decelerated, which the authors suggested may be because of soil saturation. Duval *et al*. (2012) found a similar threshold for abundance of *Typha* in fen communities in Ontario, with approximately linear increases in abundance up to 60 mg/L of soil phosphate and invasion slowing at higher concentrations. In the Holland Marsh, such a threshold does not yet appear to have been reached (Figure 4a).

Eutrophication, however, is not the only stress in this fen. As with many wetlands remaining in southern Ontario, the Holland Marsh wetland also experiences ongoing stresses associated with expansion of agricultural production, infrastructure development, and local changes to hydrology (Kissel and Choi 2018). In the case of this fen specifically, a network of berms and canals was constructed beginning in the late 1970s along this study site's western boundary as well as ~800 m to the south. Shortly thereafter the greatest rate of shrub expansion occurred in the fen (Figures 2, 3), perhaps associated with a lowering of the water table on the fen's western side, and an interruption of the flow of groundwater rich in calcium and other minerals to this area (MTO 1984).

Hydrologic changes may also be contributing to the expansion of *Typha* in this wetland. As demonstrated by Wilcox *et al*. (2008) and Wilcox and Bateman (2018), an increase in both water levels and water level stability has been associated with *Typha* expansion in wetlands on Lake Ontario. My study site is immediately adjacent to Lake Simcoe, whose water levels have been managed since 1918. Water level management has included an increase in overall depth of water in the lake, and a greater stability in water levels, particularly since 1966 (Environment Canada 2021).

Much effort has been expended to reduce P loading in the Lake Simcoe watershed (North *et al*. 2013; Davidson and de Loë 2016). Although the primary

objective of P reduction has been to protect the reproduction of coldwater fish in the lake (North *et al.* 2013), reductions in P loads may also help protect this fen ecosystem. Unfortunately, however, even after the cessation of surface water loadings, P in wetland soils can still spread further into upland areas, because of cycling through plants and detrital material (Koch and Reddy 1992; Bostic *et al.* 2010) and internal eutrophication (Boers and Zedler 2008). As such, active restoration efforts may be necessary to stop the spread of *Typha* in these systems through actions, such as the harvesting of *Typha* shoots and removal of its leaf litter. These actions have been shown to allow *Carex* to recolonize cleared habitat, albeit at a relatively slow rate of expansion (Hall and Zedler 2010; Larkin *et al.* 2012; Lishawa *et al.* 2015; Wilcox *et al.* 2018).

Bradford (2016) argued that watershed-scale approaches to wetland conservation are necessary to understand and manage the impacts that land-use change has on wetland hydrologic regimes. At Holland Marsh, the expansion of *Typha angustifolia* associated with P loading from upstream land use and the reduction in extent of a rare Cyperaceae-dominated fen community gives further support to this argument. The conservation and management of wetlands in landscapes with high levels of human pressure should consider the impacts that land use in the entire watershed has on communities of rare and endangered plants and animals.

Acknowledgements

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The Canadian Field-Naturalist welcomes our new Book Review Editor

Starting with Issue 136, Volume 1, *The Canadian Field-Naturalist* will have a new Book Review Editor, Jessica Sims (bookrevieweditor@canadianfield naturalist.ca). While we transition from the interim editors (Amanda Martin and William Halliday), readers of this journal are invited to request titles they are willing to review from the list from Jessica and, if still available, copies will be sent directly to them by the publisher. Readers will still be able to submit reviews of books they have on hand, provided that reviewed books have a Canadian connection, including those on any species (native or non-native) that inhabits Canada, as well as books covering topics of global relevance, including climate change, biodiversity, species extinction, habitat loss, evolution, and field research experiences. Book reviews will be submitted through the online submission system https://www.canadianfieldnaturalist.ca/index.php/cfn/about/submissions. All received reviews will undergo editing, and prospective reviewers are encouraged to check our book review guidelines at https://www.canadianfieldnaturalist.ca/index.php/cfn/about/sub missions.

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.

ZOOLOGY

We Are All Whalers: the Plight of Whales and our Responsibility

By Michael J. Moore. 2021. University of Chicago Press. 224 pages, 25.00 USD, Cloth, E-book.

Large whales around the world have been under constant threat from human activities for centuries. Commercial whaling reduced most populations of whales to very low numbers until the mid-20th century. Since the end of most global commercial whaling, many populations have recovered to some extent. However, many whales now face new threats from commercial fishing and marine vessel traffic. Whales that enter commercial shipping lanes can be struck by vessels (known as ship strikes or vessel strikes), resulting in serious injury and often death, and whales that interact with commercial fishing gear (ropes, nets) can become entangled, which also causes injury that can lead to death if the whale remains entangled for long periods. Both ship strikes and entanglement are serious concerns for one whale species in particular, North Atlantic Right Whale (NARW; *Eubalaena glacialis*). NARW were a popular target species for commercial whalers and were nearly driven to extinction, but have since rebounded to just over 400 individuals. However, in the past four years (2017–2021), at least 50 NARW have died or have been seriously injured, leading to population size estimates of <350 individuals (NOAA 2021). All of these injuries and deaths with known causes were from ship strikes and entanglement with fishing gear. NARW are in a crisis right now, therefore it is crucial to find solutions to reduce these unnecessary mortalities and injuries to this species. This crisis for NARW, as well as similar entanglement and ship strikes to other whale species, is the impetus behind *We Are All Whalers*.

This book is not just about NARW: it is also a bit of an autobiography of the author, Michael Moore, although that it is not its main purpose. The book gives a lot of background on Moore: his training, experiences, and what led him to the thesis of the book, which is that more needs to be done to protect NARW. The book is filled with very interesting stories and, for those like me who study whales, many familiar names pop up throughout the book as Moore interacted and collaborated with many very well-known whale researchers throughout his career. The most striking of these stories to me was Moore's first season at sea doing fieldwork, where he was a research assistant for Hal Whitehead, a world-renowned whale biologist who at that time was a Ph.D. student studying Humpback Whale (*Megaptera novaeangliae*). Moore's amazing experiences during that first field season are likely largely responsible for his focus on whales throughout his career. Although many of the stories in the early chapters of the book are not focussed on NARW, these stories add interesting context on Moore's journey from naïve student to experienced wildlife veterinarian and biologist. I found these stories really enjoyable to read, even though they were not relevant to NARW; this is likely because I am a biologist who enjoys fieldwork. There is even an entire chapter devoted to a trip that Moore took to Utqiaġvik, Alaska, to learn about Bowhead Whales (*Balaena mysticetus*) harvested as part of the subsistence hunt by the Iñupiat of that region. This chapter certainly stood out to me, because I study that particular population of whales. Moore uses his experience in Utqiaġvik to make the argument that if people who harvest whales for subsistence, like the Iñupiat, can also co-exist with those whales and not negatively affect the population, then people who are not harvesting whales should be able to do the same.

All of the context provided in the early chapters of this book sets up Moore's expertise and adds credibility to the main arguments that he makes in the book. Moore was trained as a veterinarian at University of Cambridge and obtained his Ph.D. in biological oceanography from Massachusetts Institute of Technology and Woods Hole Oceanographic Institution. He was involved in some of the earliest necropsies of deceased NARW on the east coast of the United States and has been involved in researching NARW, especially their mortalities, since the mid-1990s. Needless to say, he is a world-renowned expert on NARW and assessing cause of death for whales.

The title of this book was quite intriguing to me as I began reading the text but, on the surface, its meaning is perhaps not obvious. Moore's main thesis is that NARW are continuing to die due to human nature: our demand for goods and seafood is the root cause of the ship strikes and entanglements currently plaguing NARW. Even though we are not killing whales on purpose like the commercial whalers of old, our behaviour is still leading to unnecessary suffering and death of these complex, social animals. The final chapter of this book really sums up this idea and what we as consumers need to do to make a change: only purchasing seafood that is harvested in a sustainable

manner that does not threaten whales with entanglement and only purchasing goods that do not increase ship strike risk to whales. Economic pressures may very well be a powerful tool that can cause a change in the commercial fishing and shipping industries, but for it to work a large proportion of the human population would need to change their spending habits. The main point of this book was to educate the general public about the plight of NARW and other large whales and specifically make people aware of what they can do to help these animals. I sincerely hope that many people will read this book and that positive change will happen for NARW.

This book is written in a fairly accessible way; it generally avoids scientific jargon and is filled with interesting stories, so should be appropriate for a general audience, even if the reader has very little scientific knowledge. The target audience will likely be anyone with an interest in whales, conservation,

or environmentalism. Some parts of the book might be too graphic for some readers, with descriptions of whale death and injury, as well as descriptions of the necropsies performed on dead whales. However, it is certainly important for readers to understand what happens to these whales to evoke empathy. Overall, this book was a very good read, and I highly recommend it.

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WILLIAM D. HALLIDAY

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Wolves: Western Warriors

By Julie Argyle. 2022. Gibbs Smith. 224 pages, 50.00 USD, Cloth.

Wolves, similar to Argyle's book *Bears* (2021, Gibbs Smith; Way 2021a), is an impressive, coffee-table-style book. It contains about 200 glossy, colour pictures of Gray Wolf (*Canis lupus*) and scenery from Yellowstone National Park. It is a large (26.0 × 2.4 × 30.6 cm), heavy book (~2 kg) meant to be gazed at in admiration as we are given the pleasure of looking into the lives of these controversial and politically devisive animals. Fans of Yellowstone, nature, wolves and canids, predators, the western United States, and national parks will enjoy this book.
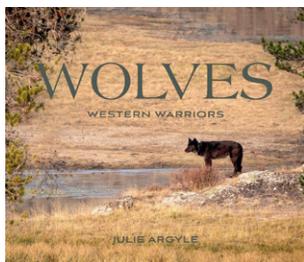
I recently read very personal accounts of Gray Wolves (e.g., Way 2020, 2021b) and Grizzly Bears (*Ursus arctos horribilis*; Way 2021a) inhabiting Yellowstone. This tome follows suit. Argyle shows her appreciation for the species by dedicating the book to her subjects, noting that wolves are sentient beings which have suffered at the hands of humankind (p. 5). She describes wolves as one of the most unique animals on the planet (p. 13), full of love, compassion, empathy, and devotion (p. 14). Particularly heartwarming to Argyle is the love wolves show for each other, along with their zest for life (p. 117). Wolves

are highly social animals that live in packs (p. 21). They are often compared to humans because we share similarities in social behaviour (p. 10) and, like humans, each wolf has a distinct personality.

In the chapter The War on Wolves, Argyle succinctly describes the awful things that humans have done to wolves over the course of recent history, as well as the efforts made to recover them in places like Yellowstone (p. 65). Wolves live a natural life in the national park, which provides protection from their biggest threat outside the park—humans (p. 71).

The earlier chapters in *Wolves* set the stage for the rest of the book, with the latter sections focussing on individuals, and showing awe-inspiring images of them. I especially liked the stunning photo of a shed out, lanky, uncollared black wolf staring at the camera as it travelled along a water body during the summertime (p. 81). Through Argyle's words and pictures, we get to know 755M, 926F, 1091F (a.k.a. Daddy's Girl), and White Lady and her mate 712M, as well as additional members from the Wapiti Lake and Lamar Canyon Packs—the two packs most frequently observed by Argyle (and most park visitors). The white alpha female of the Wapiti Lake Pack held a special place in her heart that no other wolf will ever be able to fill (pp. 117–119). Learning that this alpha female's daughter, 1091F, was killed while hunting was a difficult blow to Argyle (p. 117). The author was brought to tears both when 926F was shot by a

hunter in suspicious circumstances a mile (1.61 km) outside Yellowstone (p. 157), as well as when White Lady died from a hunter's bullet at the age of 12 at the northern park boundary (p. 193). I enjoyed reading Argyle's personal stories of these wolves which she has watched over the years, and viewing photographs emanating from those accounts was especially special.

Wolves: Western Warriors was an easy read and is well written. I read it over the period of a few hours on back-to-back days. One minor complaint I have is that there are no maps in the book. Showing the current range of the wolves in the United States, with Yellowstone National Park highlighted, would have been helpful to frame where the author took the pictures compared to the species' overall range. In addition, the pictures did not have descriptions. In some cases it was obvious which wolf we were looking at based on the chapter, but in many others it was not clear. Having short, one to two sentence, captions describing them would have been beneficial. Also, the book was relatively pricey, at $50 USD. Yet, this might be expected given the book's large dimensions and the 100% glossy paper used for all 224 pages.

Overall, I really enjoyed reading *Wolves*, although it is difficult for me to not like anything that is Yellowstone-based, especially when it involves wolves. At the end of the book, Argyle noted that wolves have the same emotions as you and me, so we need to be a voice for them (p. 205). I hope we all heed the author's suggestion, and speak up and demand better protections for this sentient, social, and emotional animal.

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

Way, J. 2021a. [Book Review] Bears: The Mighty Grizzlies of the West, by Julie Argyle. Canadian Field-Naturalist 135: 321–322. https://doi.org/10.22621/cfn.v135i3.2875

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JONATHAN (JON) WAY

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NEW TITLES

Prepared by William Halliday

Please note: All books listed are available for review at the time of this publication. Please contact the Book Review Editor, Jessica Sims (bookrevieweditor@canadianfieldnaturalist.ca), if you are interested in reviewing any of these or any other new book.

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

BOTANY

Luschiim's Plants: Traditional Indigenous Foods, Materials and Medicines. By Luschiim Arvid Charlie and Nancy Turner. 2021. Harbour Publishing. 288 pages, 29.95 CAD, Paper.

The Science and Spirit of Seaweed: Discovering Food, Medicine and Purpose in the Kelp Forest of the Pacific Northwest. By Amanda Swinimer. 2021. Harbour Publishing. 256 pages, 28.95 CAD, Paper.

CONSERVATION AND CLIMATE CHANGE

Effective Conservation: Parks, Rewilding, and Local Development. By Ignacio Jiménez. 2022. Island Press. 280 pages, 45.00 USD, Paper, 44.99 USD, E-book.

ZOOLOGY

Bats of British Columbia. By Cori Lausen, David Nagorsen, Mark Brigham, and Jared Hobbs. 2022. Royal BC Museum. 384 pages and 312 colour photographs, 34.95 CAD, Paper, 19.99 CAD, E-book.

Whelks to Whales: Coastal Marine Life of the Pacific Northwest. Third Edition. By Rick M. Harbo. 2022. Harbour Publishing. 352 pages, 28.95 CAD, Paper.

ORNITHOLOGY

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

OTHER

Applied Panarchy: Applications and Diffusion across Disciplines. By Lance H. Gunderson, Craig R. Allen, and Ahjond Garmestani. 2022. Island Press. 352 pages and 30 illustrations, 49.00 USD, Paper, 48.99 USD, E-book.

The Hidden Kingdom of Fungi. By Keith Seifert. 2022. Greystone Books. 288 pages, 34.95 CAD, Hardcover.

Vancouver, Howe Sound & the Sunshine Coast, Fourth Edition, 2022: Including Princess Louisa Inlet & Jedediah Island. By Anne Yeadon-Jones and Laurence Yeadon-Jones. 2022. Harbour Publishing. 192 pages, 49.95 CAD, Paper.

Voles, Not Moles. By Soren Bondrup-Nielsen. 2021. Gaspereau Press. 240 pages, 29.95 CAD, Paper.

Woman, Watching: Louise de Kiriline Lawrence and the Songbirds of Pimisi Bay. By Merilyn Simonds. 2022. ECW Press. 400 pages, 36.95 CAD, Hardcover.

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

2022 Joint Southeastern Branch and American Phytopathological Society-Caribbean Division Meeting

The 2022 Joint Entomological Society of America, Southeastern Branch and American Phytopathological Society-Caribbean Division Meeting to be held 26–30 March 2022 as a hybrid event, with online content and an in-person meeting at the Sheraton Puerto Rico Hotel & Casino, San Juan, Puerto Rico. The theme of the meeting is: 'Creating and Renewing Connections'. Registration is currently open. More information is available at https://www.entsoc.org/membership/branches/southeastern/meeting.

Northeast Fish & Wildlife Conference

The 77th annual Northeast Fish & Wildlife Conference, hosted by the New Jersey Department of Environmental Protection's Division of Fish and Wildlife, to be held 3–5 April 2022 as a hybrid event, with online content and an in-person meeting at the Ocean Place Resort, Long Branch, New Jersey. The theme of the conference is: 'The Power of Partnerships for Landscape Level Planning'. Registration is currently open. More information is available at https://www.neafwa.org/conference.html.

Entomological Society of America, Pacific Branch Meeting

The annual Pacific Branch Meeting of the Entomological Society of America to be held 10–13 April 2022 at the Hyatt Regency Sonoma Wine Country, Santa Rosa, California. Registration is currently open. More information is available at https://www.entsoc.org/membership/branches/pacific/meeting.

IALE-North American Annual Meeting

The annual meeting of the North American Regional Association of the International Association for Landscape Ecology (IALE-NA) to be held as an online meeting 11–14 April 2022. The theme of the meeting is: 'The Next Generation of Landscape Ecologists — Supporting our Future'. Registration is currently open. More information is available at https://www.ialena.org/annual-meeting.html.

Northeast Natural History Conference

The Northeast Natural History Conference to be held 22–24 April 2022 at the Albany Capital Center, Albany, New York. Registration is currently open. More information is available at https://www.eagle hill.us/NENHC_2022/NENHC2022.shtml.

2022 Joint Aquatic Sciences Meeting

The 2022 Joint Aquatic Sciences Meeting to be held 14–20 May 2022 at the DeVos Place convention centre, Grand Rapids, Michigan. The theme of the meeting is: 'Rapid Changes ~ Collaborative Solutions'. Registration is currently open. More information is available at https://jasm2022.aquaticsocieties.org/.

Ontario Ecology, Ethology, and Evolution Colloquium

The 52nd annual Ontario Ecology, Ethology, and Evolution Colloquium, hosted by Queen's University, to be held 25–27 May 2022 as a hybrid event, with online content and an in-person meeting in Kingston, Ontario. More information is available at https://oe3c.com/.

In Memoriam: Jeffrey A. Hutchings, FRSC (11 September 1958–30 January 2022)

Dalhousie University Professor of Biology and the Izaak Walton Killam Memorial Chair in Fish, Fisheries and Oceans died suddenly and unexpectedly in Halifax, Nova Scotia. Dr. Hutchings was a world-class biologist best known for linking fundamental principles from life-history theory with implications for sustainability of marine fisheries and his critique of Fisheries and Oceans Canada explanations for the cause of the Atlantic Cod (*Gadus morhua*) collapse. He was a member of the Committee on the Status of Endangered Wildlife in Canada for 12 years, including Chair (2006–2010). His personal reflections on his career including cod were published shortly before his death (Hutchings 2022). Details of this too-short career can be found by searching his name on the web.

Literature Cited

Hutchings, J.A. 2022. Tensions in the communication of science advice on fish and fisheries: northern cod, species at risk, sustainable seafood. ICES Journal of Marine Science: fsab271. https://doi.org/10.1093/icesjms/fsab271

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

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Compiled by William Halliday

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The CANADIAN FIELD-NATURALIST

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