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COVER: Common Raven (*Corvus corax*) in Kugluktuk, Nunavut, Canada. See the article in this issue by Myles Lamont, pages 254–260. This species was not one of the 10 birds newly documented as nesting near the community since 2016 and is one of the few year-round avian residents. It is commonly found in communities across the Canadian Arctic. Photo: Myles Lamont, February 2016.

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Divorce in Canada Geese (*Branta canadensis*): frequency, causes, and consequences

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Abstract

Most Canada Geese (*Branta canadensis*) form lifelong pair bonds (same-mate geese), but some pairs break apart and the geese mate with new partners while their former mates are still alive (divorcees). Over 25 years, we assessed lifelong reproduction of 160 collared Canada Geese that nested for multiple years in New Haven County, Connecticut. We examined whether same-mate geese and divorcee geese differed from each other prior to or after the divorce. Fifteen percent of females and 18% of males divorced during their lifetimes. Divorces were more frequent in pairs that produced fewer hatchlings during their prior nesting year. Most divorcees that nested again did so on their former nesting territories. Replacement partners of divorcees averaged younger and had fewer years of nesting experience than the divorcees' prior mate. Usually after a divorce, one divorcee of each former pair nested immediately while the other skipped one or more years before nesting again. Under such circumstances, the partner able to nest immediately can increase its direct fitness by finding a new partner and nesting rather than foregoing the opportunity to nest that year. During their first nesting year after the divorce, the reproductive success of divorcees and same-mate geese were similar.

Key words: Canada Geese; lifelong reproduction; mate fidelity; mate selection; monogamy; pair bonds

Introduction

Many bird studies have found a positive relationship between the duration of a pair bond and the pair's reproductive success (Pyle *et al.* 2001; van de Pol *et al.* 2006). Black (2001) and Cooke *et al.* (1981) hypothesized that this was because mates were able to coordinate their behaviour so they are better able to watch for predators, defend their nesting territory from conspecifics, and provide their young with access to better foraging areas. Despite the advantages of a durable pair bond, some individuals pair with a new partner while their former partner is still alive. We refer to this as a divorce and the individuals as divorcees, terms widely used in the ornithological literature (Ens *et al.* 1993; Dhondt and Adriaensen 1994; Choudhury 1995).

Several hypotheses explain divorce in species that normally have lifelong pair bonds. Owen *et al.* (1988) hypothesized that a divorce results when a pair becomes separated during winter or migration, and one mate reached the nesting grounds before the other and pairs with a new bird before its former mate arrives (lost-mate hypothesis). The incompatible-mates hypothesis argues some geese cannot work well together when nesting due to individual incompatibilities, but these same individuals could be good partners for other geese (Coulson 1972; Choudhury 1995; Dhondt 2002). The territorial-improvement hypothesis predicts that divorces occur when one mate has the opportunity to gain access to a better territory by switching mates (Dhondt and Adriaensen 1994; García-Navas and Sanz 2011) while the mate-improvement hypothesis argues that divorces result when one mate has an opportunity to mate with a better partner (Ens *et al.* 1993; Choudhury 1995).

Geese and swans (Anatidae) are renowned for their lifelong pair bonds; most geese and swans have only one mate during their entire lives (Bellrose 1980; Baldassarre 2014). Yet, some pairs break apart while both mates are alive and in the same area, and the former mates reproduce with others. The frequency of divorce (proportion of pairs that divorce) was <2% in Lesser Snow Geese (*Chen caerulescens caerulescens*; Cooke *et al.* 1981), <2% in Richardson's Cackling Geese (*Branta hutchinsii hutchinsii*; MacInnes and Lieff 1968), 7% in Canada Geese (*Branta canadensis*; Raveling 1988), and 8% among Barnacle Geese (*Branta leucopsis*; Black *et al.* 1996). Among swans, divorce rates were 0% in Bewick's Swans (*Cygnus bewickii*), 3.7% in Mute Swans (*Cygnus olor*), and 5.8% in Whooper Swans (*Cygnus cygnus*; Rees *et al.* 1996). Baldarrasse (2014) is the authority for the names of subspecies in this paper.

For 25 years, we studied a marked (collared) population of Canada Geese located in Connecticut to determine the frequency of divorce, why some geese divorce while others remain with their prior mates, and the consequences of divorce. We tested the hypotheses that 1) the new partners of divorcees were older and had more years of nesting experience than their former mates (Ens *et al.* 1993; Choudhury 1995), 2) divorcees were unable to retain their prior nesting territory because a single bird cannot defend a territory alone (Abraham *et al.* 1981), 3) divorces are more common in pairs that had experienced reproduction failures (Coulson 1972), and 4) divorcees were less successful reproducing than geese that remained with their prior mates (Catry *et al.* 1997).

Methods

We examined reproduction of Canada Geese (*Branta canadensis*) in New Haven County, Connecticut, USA (centroid: 41.3267°N, 72.89043°W). The terrain is mostly flat near the coast of Long Island Sound but rises to low hills (up to 320 m) in the northern part of the county. The county has numerous ponds, streams, and rivers. Several reservoirs have been created to provide power or store water.

Canada Geese started nesting in New Haven County during the late 1970s (Conover and Chasko 1985). These geese were non-migratory and rarely left the county once they started nesting (Conover 2012). We started banding these geese and studying their movements, survival, and reproductive success in 1984 and continued through 2008.

Most Canada Geese in the county built their nests on islands, abandoned Muskrat (*Ondatra zibethicus*) lodges, and abandoned Mute Swan nests scattered throughout the county but brought their broods to one of three brood-rearing sites, sometimes travelling several kilometres to reach them (Conover 2012). Each brood-rearing site was located on a reservoir complex of two to four lakes. The three complexes were Konold's Pond-Lake Dawson, Whitney Lakes, and Maltby Lakes. Adjacent to these lakes were golf courses, shopping centres, and apartment buildings. The broods usually foraged on the lawns associated with these areas (Conover and Kania 1991). For instance, the broods from Maltby Lake complex spent most of their time on Yale University Golf Course, which offered both rich foraging grounds (lawns) and sanctuaries (water hazards and ponds; Conover 2012).

In Connecticut, Canada Goose eggs hatch in late April and early May, and goslings fledge in early July (Conover and Frank 2018). Adult geese moult their primary feathers and become flightless in late June. During the moult, we rounded up goslings and adults at all brood-rearing areas in New Haven County by herding them into funnel traps (Smith *et al.* 1999). We weighed each bird upon capture, determined its sex through a cloacal examination, and banded it with a U.S. Geological Survey (USGS) aluminum leg band and either a large leg band or neck collar made of plastic by Spinner Plastics (Springfield, Illinois, USA). Each large leg band and neck collar had a unique combination of letters and numbers large enough (letters were 1.3 cm in height on leg bands and 3 cm on collars) so we could identify individuals from far enough away that our presence did not disturb the geese. Collars were identical to those used extensively throughout the Atlantic Flyway (Hestbeck and Malecki 1989). We replaced worn or lost leg bands or neck collars by identifying individuals by their USGS leg bands. We searched Connecticut for geese wearing large leg bands and neck collars year-round and observed most birds dozens of times each year. We also used sightings of marked geese reported to the U.S. Bird Banding Lab to locate birds. Once Canada Geese started nesting, they exhibited great fidelity to nesting and brood-rearing areas; only one goose we observed nesting in New Haven County was ever observed nesting outside the area (Conover 2012). We considered a female to have reproduced during any year that it was observed incubating a nest or attending a brood and a male to have reproduced during any year that it was observed attending a brood or defending a territory in which a female was incubating a nest.

All geese were banded by us when they were goslings (HY geese) or adults (AHY geese) prior to 2001; those born after 2001 were excluded from the analysis because we were interested in the long-term consequences of divorce. We knew the age of all HY geese, but not for AHY geese. Because most Canada Geese breeding in the area were banded as goslings, most birds first captured as adults were probably relatively young (i.e., one to three years old). Hence, we assumed each AHY goose was two years old when first banded. Including AHY geese in our study introduced some imprecision into the aging of geese. Previously, Conover (2012) assessed whether any bias was created by including AHY geese in the database and found HY and AHY geese were similar in all measures of age-related reproduction.

We visited every known Canada Goose nest in New Haven County to determine clutch size. Goose nests were located by flights over the county by Connecticut Department of Environmental Protection staff and by searching all water bodies appearing on USGS topographical maps from shore or a boat. Most nests were discovered by observing a lone male. We observed each nest from a distance at least weekly to determine if it was still being incubated. We mapped nesting territories each year by noting the location of both mates during the incubation period and where they confronted intruding geese. Usually the territory consisted of a small island or shoreline and the water around it. Sometimes, we recorded the exact location of nesting territories, but not always.

We determined brood sizes at least twice a week for the first month after hatching and then every week or two until the goslings could fly in July. Broods were identified by the parents that were attending them. Individual goslings were not marked at hatching, but broods were individually dyed or marked with ink at hatching when multiple broods were at the same place so we could keep track of goslings. We assumed all goslings in a brood died when the parents were observed without their brood, provided that 1) none of their marked goslings were observed with another brood and 2) no other brood at the same site increased in size when the brood disappeared.

We recorded brood sizes at hatching and fledgling. We defined brood size at hatching as the number of goslings in a brood when first sighted (usually within 48 hours of hatching), and brood size at fledging as the number of goslings in a brood the day before we captured the parents and brood, which took place immediately before the goslings gained the ability to fly. We recorded whether the parents raised their brood by themselves (two-parent family) or whether they joined with other parents to form a gang brood. A gang brood occurred when two or more families joined together with their offspring, resulting in a cohesive group of young accompanied by four or more parents (Conover 2009). The number of fledglings in a gang brood was divided by the number of adult pairs attending the brood to determine the number of fledglings each pair produced, with the provision that the number of fledglings assigned to a pair could not exceed its brood size at hatching.

We identified nesting adults by their band or collar numbers and determined their age, the age and identity of their mates, clutch size, brood size at hatching, and brood size at fledging. We noted if the marked geese had nested on the same territory during prior years.

Usually, paired geese nested together year after year, but sometimes, we found a banded goose nesting with a new partner while its former partner was still alive and in the area. We defined this as a divorce. At least one of the prior partners had to nest again because otherwise we would not know a divorce had occurred. We wanted to compare divorcees to other geese that remained paired with their former mates (same-mate geese). There were two criteria for a nesting goose to be a subject for this study (i.e., either a divorcee or same-mate geese). First, both the subject and its mate had to wear either a large leg band or neck collar so that we could individually recognize them. Second, a subject had to nest at least two years during its life so that it had the opportunity to switch mates from one year to the next and its former mate had to be alive and in the area during the second year the subject nested. All geese that met these criteria in New Haven County were included in this study.

We determined the divorce rate, which is the proportion of subjects that became a divorcee anytime during their lives, and the annual divorce rate, which is the proportion of nesting birds that initiated a divorce from one year to the next. The annual divorce rate was calculated as the number of divorcees divided by the total number of nest-years by subjects after their first nesting year. Each subject's first nesting year was excluded from this analysis because a divorce cannot occur during the first nesting year. We compared the frequency of divorce among females and males using a 2 × 2 contingency test corrected for continuity (Siegel 1956). Results were considered statistically significant when $P \leq 0.05$. We hypothesized that some divorces result when a goose that has nested during a prior year has an opportunity to move to a better nesting territory by divorcing its former mate and mating with a new partner that had a better territory. To test this hypothesis, we determined the number of divorcees that remained on the same territory they had prior to the divorce.

In Canada Geese, reproductive performance is positively correlated with parental age and nesting experience (Baldassarre 2014), and we hypothesized that divorces result when one mate has the opportunity to nest with an older, more experienced goose than its current mate. We used a paired t-test (Siegel 1956) to compare the age and years of nesting experience of a divorcee's replacement mate (i.e., the individual a divorcee nested with after its divorce) during its first nesting year with the divorcee against the age and prior nesting experience of divorcee's prior mate (i.e., the individual a divorcee nested with prior to its divorce) during that same year.

Divorce prediction analyses

Factors predicting the probability of divorce were evaluated with binary generalized linear models (GLM). Same-mate geese were coded as the reference category. Models with all possible combinations of age, sex, mass, and reproductive success prior to divorce were compared using Akaike Information Criterion adjusted for small sample sizes (AICc) and Akaike weights (w_i). Metrics of reproductive success were highly correlated; thus, we selected the best metric for reproductive success by comparing single-variable models with AICc. Only the reproductive success variable with the lowest AICc was used in models with age, sex, and body mass to predict divorce. We used these models to test the hypotheses that divorces were more frequent among pairs that had been less successful during their last nesting attempt or during all nesting attempts in the past or when one of the partners was in poor body condition.

Divorce consequence analyses

We used binary GLMs to compare divorcees to same-mate geese to determine the reproductive benefits or costs of a divorce. Same-mate geese were coded as the reference category. For this analysis, we compared reproductive success of divorcees to same-mate geese after divorce. We also used variables describing the change in these reproductive success variables from before divorce to after divorce; these variables describing change were calculated as reproductive success after divorce minus reproductive success prior to divorce (e.g., brood size during the year after the divorce minus brood size the year prior to divorce). Models with all possible combinations of age, sex, reproductive success after divorce, and change in reproductive success were compared with AICc and w_i. To avoid auto-correlation of reproductive success metrics, we selected the best metric for reproductive success after a divorce (brood size at hatching, or brood size at fledging the year after a divorce or the number of fledglings produced during all nesting years following a divorce) by comparing single variable models with AICc. The same procedure was conducted to select the best predictor of change in reproductive success. We used the best post-divorce reproductive variable and the best change in reproductive success variable based on AICc to compare the reproductive consequences of divorce.

All GLMs were evaluated using statistical program R (R Core Development Team 2015). For divorce prediction and divorce consequence analyses, we report on variables that were informative (85% CI of parameter estimates that did not overlap 0) and variables that were highly precise (95% CI of parameter estimates that did not overlap 0). For the divorce consequence analysis, we compared the nesting year following a divorce for divorcees with the nesting year following the randomly selected year for same-mate geese. Likewise, we compared for divorcees all nesting years following a divorce with all nesting years following the selected nesting year for same-mate geese.

Results

We banded 858 females of which 207 nested at least once, and 883 males of which 152 nested at least once. We observed 84 females and 76 males that nested for multiple years; these were the subjects of this study. Among them, 13 females (15%) and 14 males (18%) divorced; the divorce frequency did not differ between sexes ($\chi_1^2 = 0.25$, $P = 0.62$). The annual divorce rate was 7.6% for females based on 172 nest-years and 7.3% for males based on 190 nest-years (first nesting years were not included because birds cannot divorce during their first nesting year). Annual divorce rates were similar among female and male subjects ($\chi_1^2 = 0.01$, $P = 0.95$). No divorcee ever returned to its original partner following a divorce.

Prior mates of female divorcees were older ($t_{10} = 2.21$, $P = 0.05$) and had more years of nesting experience ($t_{10} = 4.66$, $P = 0.001$) than the replacement mates of female divorcees; prior mates were 7.8 ± 3.9 (mean ± SD) years old and had 3.3 ± 3.6 years of experience while the replacement mates were 5.0 ± 3.2 years old and had 1.1 ± 1.0 years of experience. Male divorcees' prior mates also were older ($t_{11} = 2.76$, $P = 0.02$) and had more years of nesting experience ($t_{11} = 2.86$, $P = 0.02$) than the replacements; prior mates were 7.8 ± 3.9 years old and had 3.3 ± 3.6 years of experience while replacement mates were 5.0 years old and had 1.1 ± 1.0 years of nesting experience.

We often did not record the exact location of nesting territories, but for four male and four female divorcees we noted the nesting territories before and after their divorce. All of the males retained their former nesting territories after their divorces, as did three females. For the one female exception, its former partner retained its former nesting territory, and the female divorcee moved to a new nesting territory on an island in an adjacent lake.

Divorce prediction analyses

Our GLMs indicated body mass prior to divorce was a poor predictor of the probability of divorcing. Thus, body mass was excluded from AIC modeling. We used the brood size at hatching in our GLM modelling because it was the best reproductive metric for predicting divorce.

Our best GLM for predicting divorce had $w_i = 0.28$ and indicated pairs with small broods at hatching were more likely to divorce in the subsequent year (Table 1). Future divorcees produced fewer hatchlings prior to divorce than same-mate pairs (parameter estimate = −0.18 [95% CI = −0.38–0.00]). However, the best GLM model was only 1.67 AICc lower than the intercept-only model indicating while the effect of brood size at hatching was a precise predictor (based on 95% CI) of the probability of divorce, the model did not account for much of the variance in the data. Although two models that included age prior to divorce (ΔAICc = 0.92, $w_i = 0.18$ and ΔAICc = 1.5, $w_i = 0.13$) had w_i similar to our top AICc model, age had parameter estimates with 85% CI that widely overlapped zero in both models. No model with sex was better than the intercept-only model (Table 1). This indicated age prior to divorce and sex was not different among same-mate geese and geese that divorced.

Divorce consequences analyses

We compared the reproductive success of 23 divorcees (13 females and 10 males) to 110 same-mate geese (58 females and 52 males) during their first nesting year after the divorce. We used brood size at hatching during the year following divorce, the difference in number of fledglings in the final nesting year before divorce, and number of fledglings in the next nesting year after divorce in AIC modelling to compare geese that divorced to geese that nested a second year with their former mate. Although multiple models that also included age post-divorce, sex, and/or change in fledglings per nesting years were within ΔAICc = 4 and cumulative $w_i = 0.95$ (Table 2), all of these variables had parameter estimates with 85% CI that overlapped zero in both models. Thus, we decided to only discuss the top model as the most parsimonious description of the consequences of divorce. Our best GLM for assessing the consequences of divorce had $w_i = 0.22$ and indicated divorcees had smaller brood sizes at hatching and more years of nesting hiatus compared to same-mate geese (Figure 1). The poor fit of any change in reproductive success variable indicated neither divorcees nor same-mate geese had increased reproductive success with successive nesting years.

Discussion

Canada Geese are long-lived. In New Haven County, Connecticut, 15% of nesting geese that were recruited

TABLE 1. Results of generalized linear models comparing Canada Geese (*Branta canadensis*) that will divorce their mates during their next nesting year (13 females and 14 males) to geese that will remain paired with their prior mate during their next nesting year (58 females and 52 males). Models were used to determine why some geese divorce but not others. Models were compared with Akaike Information Criterion adjusted for small sample sizes (AICc) and Akaike weights (w_i). Data were from the divorcees' last year with their prior mate compared to the same-mates' first of two years nesting with the same mate. Dependent variables included the subjects' age, sex, and brood size at hatching. Data were collected in New Haven County, Connecticut (1984–2008).

Models	K	ΔAICc	w_i	Deviance
Brood size at hatch*	2	0.00	0.28	132.26
Brood size at hatch + age	3	0.92	0.18	131.10
Age	2	1.50	0.13	133.76
Intercept only	1	1.67	0.12	135.99
Brood size at hatch + sex	3	1.96	0.11	132.13
Brood size at hatch + age + sex	4	2.81	0.07	130.86
Age + sex	3	3.22	0.06	133.39
Sex	2	3.55	0.05	135.81

*AICc = 136.40.

Table 2. Top 10 generalized linear models comparing divorced Canada Geese (*Branta canadensis*; 13 females and 14 males) to geese that will remained paired with their same mate (58 females and 52 males). These models were used to determine if divorce reduces the ability of geese to reproduce. Models were compared with Akaike Information Criterion adjusted for small sample sizes (AICc) and Akaike weights (w_i). Data were from the first nesting year or all years after divorce for divorcees compared to the same-mates' second year nesting or all subsequent years with the same mate. Dependent variables included the subjects' age, sex, brood size at hatching, and change in fledglings produced per year (ΔFPY). Data were collected in New Haven County, Connecticut (1984–2008).

Models	K	ΔAICc	w_i	Deviance
Brood size at hatch + nesting hiatus*	3	0.00	0.22	120.92
Brood size at hatch + nesting hiatus + age	4	0.75	0.15	119.55
Brood size at hatch + ΔFPY + nesting hiatus	4	1.59	0.10	120.39
Brood size at hatch + nesting hiatus + sex	4	1.83	0.09	120.63
Brood size at hatch + ΔFPY + nesting hiatus + age	5	2.40	0.07	119.04
Brood size at hatch + nesting hiatus + age + sex	5	2.45	0.06	119.09
Nesting hiatus + age	3	3.18	0.04	124.10
Nesting hiatus	2	3.32	0.04	126.33
Brood size at hatch + ΔFPY + nesting hiatus + sex	5	3.50	0.04	120.14
ΔFPY + nesting hiatus	3	4.04	0.03	124.96

*AICc = 127.10.
Intercept only AICc = 138.00.

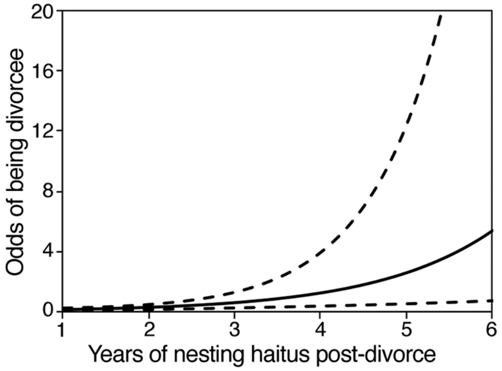

FIGURE 1. Predicted odds of Canada Geese (*Branta canadensis*) being a divorcee (solid lines) compared to a same-mate pair with 95% CI (broken lines) from generalized linear models comparing post-divorce or second year reproductive measures (divorcees to same-mate pairs, respectively).

into the breeding population lived more than 15 years, and 3% lived more than 20 years (Conover 2013). Despite their longevity, most Canada Geese nest with only one mate during their lives; 15% of females and 18% of males divorced during their lives. Raveling (1988) reported a 7% divorce rate among Canada Geese nesting in Manitoba, Canada.

Several hypotheses have been proposed to explain why divorces occur (Table 3). Owen *et al.* (1988) reported most divorces in Barnacle Geese resulted from pairs that became separated during migration or on the wintering grounds and were unable to find each other (the lost-mate hypothesis). This hypothesis, also called the asynchronous-arrival hypothesis for species where mates remain apart during the winter and reunite on the breeding grounds, does not explain divorce among our subjects. In New Haven County, Canada Geese are year-round residents; any pairs that became separated could easily relocate each other. During fall and winter, geese roost in large groups on large waterbodies (e.g.,

Table 3. Hypotheses to explain divorce in monogamous birds.

Hypothesis	Reference	Explanation	Supported by our study?
Lost mate	Owen *et al.* 1988; Ludwig and Becker 2006	Divorce occurs when mates become separated.	No. Our geese were non-migratory and mates could find each other if separated. Nevertheless, divorces still occurred.
Incompatible mates	Coulson 1972	Some birds cannot work together as pairs due to personal differences.	No. Divorces occurred after years of successful nesting. Nest success did not increase after divorce.
Territorial improvement	Dhoudt and Adriaenssen 1994	One mate divorces to obtain a better territory.	No. Few divorcees changed territories.
Mate improvement	Ens *et al.* 1993; Choudhury 1995	One mate divorces to obtain a higher-quality mate.	No. Quality of new mates were similar to former mates. Nesting success did not increase after a divorce.
Unwilling partner	Our study	Divorces occur during a year when one goose is willing to nest but its partner is not.	Yes. One former mate in each pair failed to nest the year after a divorce.

New Haven Harbor, Konolds Pond, and Whitney Lake in our study area). Usually, individual geese use the same roost every night unless disturbed (M.C. pers. obs.). Hence, any goose pair that became separated during the day could reestablish contact that same night.

The incompatible-mates hypothesis argues some birds cannot work well together when nesting due to individual incompatibilities, but these same individuals could be good partners for other birds (Coulson 1972; Choudhury 1995; Dhondt 2002). If this hypothesis is correct, then divorces should be more frequent among young birds than old birds, and divorces should occur soon after a pair starts nesting. This hypothesis also predicts both partners should re-nest quickly following a divorce, and the reproductive success of both partners should increase after divorce. Our results do not support this hypothesis because nesting success of divorcees was similar before and after the divorce. Divorcees were not younger than same-mate geese, and divorce often occurred after pairs had nested together for several years. In contrast to our findings, Raveling (1988) reported that the four divorces he observed in Canada Geese all occurred after only one or two nesting seasons with their former partners.

The territorial-improvement hypothesis predicted that divorces occur when one mate (the initiator) switched to a new mate to gain access to a better territory (Dhondt and Adriaensen 1994; García-Navas and Sanz 2011). In Eurasian Magpies (*Pica pica*) and European Nuthatches (*Sitta europaea*), divorce resulted when a neighbouring bird with a higher-quality territory disappeared. In this situation, a male with a lower-quality territory abandoned its partner to pair with the widow and take over the higher-quality territory (Baeyens 1981; Matthysen 1990). Also supporting this hypothesis were the findings of Heg *et al.* (2003) that European Oystercatchers (*Haematopus ostralegus*) with low-quality nesting territories were more likely to divorce than birds with high-quality territories. We located the nesting territory for eight divorcees both before and after the divorce; all but one occupied the same territories both before and after the divorce. Hence, our results do not indicate Canada Geese divorce to obtain a better territory.

The mate-improvement hypothesis predicted divorces resulted when one mate tries to increase its reproductive success by switching to a higher-quality mate (Table 3). However, we found that the previous mates of divorcees were both older and had more years of nesting experience than did their replacements. Furthermore, this hypothesis predicted the reproductive success of divorcees should increase after a divorce (Ens *et al.* 1993). However, we found divorces did not improve reproductive success. In Barnacle Geese, divorcees produced fewer young with their new mates than they had during their last year with their former spouse, but this was only true for their first year of nesting with their new mate (Owen *et al.* 1988; Forslund and Larsson 1991).

Out of 23 divorced pairs, we found one member of each divorced pair failed to nest during the year of the divorce with only one exception. This suggests at least some divorces occur when one mate is willing and able to nest, but its partner is not. We propose this as a new hypothesis to explain divorce in Canada Geese: the unwilling-mate hypothesis. That is, divorces occur during a year when one mate wants to reproduce, and its partner does not. Under such circumstances, the willing partner can increase its direct fitness by finding another mate and reproducing rather than foregoing the opportunity to nest that year. Unfortunately, other studies did not report if both members of a divorced pair nested during the first year following the divorce.

We found divorcees were more likely to take a nesting hiatus than same-mate geese. During the first nesting year following divorce, divorcees were older than same-mate geese and produced smaller broods at hatching. In Lesser Snow Geese, divorcees and same-mate individuals were similar in their reproductive success (Cooke *et al.* 1981); the same was true in Barnacle Geese after their first year following the divorce (Black *et al.* 1996). In contrast, Great Skua (*Stercorarius skua*) divorcees fared worse than same-mate birds in annual reproduction (Catry *et al.* 1997).

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Early and late births in high-latitude populations of free-ranging Bison (*Bison bison*)

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Abstract

The timing of parturition in high-latitude populations of Bison (*Bison bison*) is not well documented, but previous observations have indicated that births do not start until mid-May and largely end in late June or early July, similar to those of other northern ungulates. In three high-latitude Bison populations in northwestern Canada, the onset of parturition occurred as early as late March and early April—5–6 weeks earlier than previously observed—and two isolated cases of late births occurred in mid-November and mid-December. Our observations suggest that the onset of parturition in high-latitude Bison can be earlier than previously known, and late births, while apparently rare, may occur. Determining whether our observations signal a substantial, lasting shift in the timing and, possibly, synchrony of parturition in high-latitude populations of Bison will require further monitoring for early-born calves.

Key words: Bison; *Bison bison*; calving; phenology; parturition

Introduction

The birthing season for ungulates living at high latitudes is short. In northern North America, parturition by most ungulates occurs within four weeks, beginning in mid-May, peaking in late May, and tapering off by mid-June (e.g., Adams and Dale 1998; Bowyer *et al.* 1998). Where the environment is distinctly seasonal, there is strong selection toward synchrony in births—both within and between species—likely in response to a short plant-growing season and, perhaps secondarily, predation pressure. Parturition outside this "birth pulse" is of interest (e.g., Rosatte and Neuhold 2006; Jacques *et al.* 2007) because it aids in better understanding plasticity in the timing of births (Keller *et al.* 2015), and it may be maladaptive if survival or fitness is compromised for early- or late-born animals (Estes 1976; Festa-Bianchet 1988).

Bison (*Bison bison*) are an apparent exception among northern ungulates in that parturition is thought to be asynchronous compared with that of sympatric ungulates (Rutberg 1984; Green and Rothstein 1993a); however, most data on the timing of parturition of Bison are from populations at lower latitudes (≤49°N). During a five-year study (1985–1989) in Badlands National Park, South Dakota, Berger and Cunningham (1994) recorded the onset of parturition by Plains Bison (*B. b. bison*) between 3 and 7 April, with a median birth date of 2–8 May. In Wind Cave National Park, South Dakota, Green and Rothstein (1993b) reported the first births of Bison on 4–7 April, peaking in late April or early May; although varying among years (n = 3; 1982–1984), the mean length of the birth season—defined as period over which 80% of births occurred—was 53.7 ± 10.2 (SE) days. In Yellowstone National Park, Wyoming, predicted parturition has varied widely among years and herds, with the onset occurring from 31 March to 12 April and 10–27 April for the Northern and Central herds, respectively (Gogan *et al.* 2005; Jones *et al.* 2010). The median date of parturition for these herds differed by 16 days (6 May and 22 May, respectively), indicating variation in the timing of births even among closely adjacent populations. In all of the above populations of Plains Bison, the length of the birthing season varied annually, but largely began in early April and concluded by mid- to late June. A few calves were born abnormally late, including into September for most studied populations of Plains Bison, and, in exceptional cases, into November in Wind Cave (Green and Rothstein 1993a) and Yellowstone (B. Pratt-Bergstrom pers. comm. January 2012) national parks.

Unfortunately, similar field data are not available for parturition dates of free-ranging Wood Bison (*B. b. athabascae*), which occur at high latitudes (>56°N), where seasonal constraints are more pronounced. Geographic variation in the timing of Bison parturition has been postulated, with the onset of parturition and median birth date later and synchronicity of births greater in northern than in southern populations (Berger and Cunningham 1994; Gogan *et al.* 2005). For mountain sheep (*Ovis* spp.), Bunnel (1982) observed a strong relation between latitude and the onset of parturition, with later dates of first births in more northern populations. Correspondingly, for Wood Bison, the onset of parturition in Wood Buffalo National Park, Alberta and Northwest Territories, was reported as 10 May (Soper 1941) and 12 May (Carbyn and Trottier 1987), notably, more than a month later than observed for Plains Bison in the contiguous USA.

Anecdotal observations from our field surveys in northwestern Canada over the past ≥16 years concur that parturition by Wood Bison largely occurs at about the same time as that for sympatric ungulates, e.g., Caribou (*Rangifer tarandus*), Moose (*Alces americanus*), although it may start earlier, i.e., early May, and end later, i.e., late June, suggesting that the timing of forage availability, i.e., spring green-up, also strongly influences the timing of calving by Bison at high latitudes. Births outside this period have not been observed. Here, we document recent observations of unusually early- or late-born Bison calves from three reintroduced populations in northwestern Canada.

Observations

Our observations were from the Aishihik population in southwestern Yukon, Canada (Jung 2015; Jung *et al*. 2015), and the Nahanni and Nordquist populations, which occur at the nexus of the Northwest Territories, Yukon, and British Columbia, Canada (Jung 2017; Jung and Larter 2017), all located between 59°N and 61°N. These populations were monitored irregularly by wildlife management agency personnel during the parturition period. We used the description of coat colour changes in Bison calves provided by Olson (2005) to crudely estimate the parturition date of those born late.

Early-born calves

On 4 April 2013, we observed a calf from the Nahanni population, which was assumed born the previous day. In 2015 and 2016, we observed Bison calves from the Aishihik population, presumably born in early April (Table 1), with the earliest calf seen on 4 April 2016. Further, in the first week of April 2016 and 2017, lactating females that had recently been suckled were observed in the Aishihik population (Table 1). Based on a physical examination of the uterine tract of two lactating Bison shot during 4–6 April 2016, these females may have recently given birth. For a lactating female shot on 5 April 2017, the predicted birth date was possibly mid-March, based on measurements of the uterus. We note, however, that lactation itself is not unequivocal evidence that the female recently gave birth, as she may have been suckling her calf from the previous year.

TABLE 1. Observations of early- and late-born Bison (*Bison bison*) calves in northwestern Canada.

Observation date(s)	Observation	Population
Early-born calves		
4 April 2013	Newborn calf near Fort Liard, Northwest Territories. Birth occurred immediately after a late-season snow storm (F. Bertrand pers. comm. April 2013). Date of parturition assumed to be 3 April.	Nahanni
27–29 April 2015	Several dozen small, reddish calves in mixed cow–calf groups during aerial surveys near Haines Junction, Yukon (R. Drummond and R. Oborne pers. comm. April 2015). Date of parturition unknown, but assumed to be early or mid-April.	Aishihik
4–6 April 2016	Several newborn calves during aerial surveys for Bison near Haines Junction, Yukon (R. Drummond and R. Oborne pers. comm. April 2016). On 4 April 2016, we observed two harvested adult female Bison from the same area that were lactating. The onset of parturition is assumed to be earlier than 4 April.	Aishihik
4–6 April 2017	Aerial surveys for Bison in the same area as in 2015 and 2016 near Haines Junction, Yukon, did not show any calves. However, on 4 and 5 April 2017, we observed two harvested adult female Bison from the same area that were lactating. Based on a physical examination of the uterine tract, onset of parturition was estimated to be 28 March for one bison (M. Vanderkop pers. comm. April 2017).	Aishihik
Late-born calves		
17 March 2005	Reddish-brown calf in a group of 11 Bison near Haines Junction, Yukon (D. Drummond pers. comm. March 2005), noticeably smaller than other calves in the area. Based on Olson (2005), we estimated that the calf was probably 10–13 weeks old when observed and, thus, likely born in mid-December.	Aishihik
7 January 2012	Small calf with a reddish coat in a group of 26 Bison near Liard River, British Columbia, about 30–40% the size of seven other calves in the group. Based on descriptions of size and colouration and photographs provided by Olson (2005), we estimate that the calf was probably 8–10 weeks old when observed and, thus, was born in early to mid-November.	Nordquist

Late-born calves

Bison born late were rarely recorded; however, we documented two instances from two populations in northwestern Canada (Table 1). These calves were substantially smaller than other calves observed, and pelage colour also differed. Based on descriptions of size and colouration and photographs provided by Olson (2005), we estimate that these calves were born in mid-December and early to mid-November (Table 1).

Discussion

Our observations provide evidence of parturition in early April, and possibly as early as late March, in at least two high-latitude populations of Wood Bison—5–6 weeks earlier than that reported from Wood Buffalo National Park (Soper 1941; Carbyn and Trottier 1987) and earlier observations for the Aishihik and Nahanni populations by wildlife management agency biologists and conservation officers.

It is uncertain whether the earlier onset of parturition that we observed has occurred previously and gone unnoticed or if there has been a shift in the date of first births in recent years. We believe that the latter is more plausible, given that observations of Bison in late March and April by wildlife management agency personnel, Bison hunters, and local residents have not included any reports of calves born earlier than May before 2013. Detailed studies of the timing of parturition in Plains Bison in more southern latitudes (Green and Rothstein 1993a; Berger and Cunningham 1994; Gogan *et al.* 2005) and other ungulates, e.g., Thinhorn Sheep (*Ovis dalli*; Rachlow and Bowyer 1991) provide evidence of annual variation that may exceed 2–3 weeks. Moreover, the onset of parturition in Bison at Yellowstone National Park has shifted from late March to mid-April over 55 years from 1941 to 1997 (Gogan *et al.* 2005; Jones *et al.* 2010), demonstrating that changes in the timing of parturition for Bison can occur over longer time scales. Whether the early births we observed indicates a shift in the timing of parturition in Bison from the Aishihik population is unknown; showing this would require further monitoring for early-born calves.

Although the onset of parturition in southern populations of Plains Bison normally occurs around early April to match the phenology of food availability (see Introduction), early births in the Aishihik and Nahanni populations have occurred while temperatures were below freezing at night and patches of snow persisted on the ground, indicating a mismatch between early births and spring green-up of forage resources. Generally, calves born earlier in the season may have an advantage over their cohorts that may last their lifetimes (Festa-Bianchet 1988), but those born early in suboptimal conditions, possibly because their mothers were in poor body condition, may not have an advantage (Berger and Cunningham 1994). In the latter case, the prognosis for their survival is poor.

Similarly, the fate of late-born Bison is unknown. However, the late-born calves observed had both survived the critical neonatal period (i.e., the first month after being born) during early winter at high latitudes, indicating that they may survive the rest of the winter. In other instances of late-born calves, it has been assumed that the mother was in poor physical condition during the peak of conception and bred later in the season when her body stores had increased. However, the fate of these early- and late-born Bison is unknown.

In conclusion, our observations are of scientific interest because they provide new information on apparently extreme birth dates for high-latitude Bison, and they demonstrate some flexibility in the onset of parturition in these populations. It appears that parturition at high latitudes may begin in late March and, in exceptional cases, extend into December. Overall, however, the timing of parturition for Bison appears to be largely synchronous with spring green-up, albeit with a wider range of dates than for other ungulates in the region.

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Habitat selection by Common Gartersnakes (*Thamnophis sirtalis*) is affected by vegetation structure but not by location of Northern Leopard Frog (*Lithobates pipiens*) prey

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Halliday, W.D., and G. Blouin-Demers. 2018. Habitat selection by Common Gartersnakes (*Thamnophis sirtalis*) is affected by vegetation structure but not by location of Northern Leopard Frog (*Lithobates pipiens*) prey. Canadian Field-Naturalist 132(3): 223–230. https://doi.org/10.22621/cfn.v132i3.1955

Abstract

Understanding the factors affecting habitat selection of species is important for effective management and for conservation because habitat selection affects fitness. We tested the competing, but not mutually exclusive, hypotheses that habitat selection of Common Gartersnakes (*Thamnophis sirtalis*) at a fine spatial scale is driven by vegetation structure or by Northern Leopard Frog (*Lithobates pipiens*) prey abundance. We conducted surveys for snakes and frogs in six, 1-ha study grids in eastern Ontario in 2014 and 2015. Common Gartersnakes used areas dominated by forbs more than expected based on availability, and used grassy areas less than expected based on availability. Gartersnakes showed no preference for sites with more frogs. Thus, vegetation structure is important in habitat selection of Common Gartersnakes, but Northern Leopard Frog abundance is not. Common Gartersnakes and Northern Leopard Frogs did have a preference for forbs, but gartersnakes do not appear to be using habitat specifically based on frog abundance at a fine scale. Future work should study habitat use by snakes over a longer period to account for high variability in frog abundance and for temporal changes in habitat structure. Future work should also examine the distribution of other prey items in relation to the distribution of snakes.

Key words: Common Gartersnake; *Thamnophis sirtalis*; Northern Leopard Frog; *Lithobates pipiens*; eastern Ontario; habitat selection; habitat structure; prey; predator; wetland

Introduction

Habitat selection by animals is important because it affects their fitness (Fretwell and Lucas 1969; Rosenzweig 1981; Morris 1988, 2003a). Individuals should make adaptive habitat selection decisions to maximize their fitness (Morris 2011). Identifying which resources are most important to a species can be a crucial step in not only understanding habitat selection and fitness, but also in the management and conservation of a species (Morris 2003a,b, 2011). Habitat selection can be defined as "the process whereby individuals preferentially use, or occupy, a non-random set of available habitats" (Morris 2003a: 2). In this study, we examined habitat selection by snakes in relation to vegetation characteristics, water levels, and amphibian abundance in wetlands near Ottawa, Ontario, Canada. The only snake species that we encountered in sufficient numbers for statistical analyses was Common Gartersnake (*Thamnophis sirtalis*), therefore our study focusses on this species.

Although *T. sirtalis* have been studied for decades, few studies have explicitly examined their habitat preferences. Nevertheless, some of the variation across their range has been described by Ernst and Ernst (2003). Carpenter (1952) found that over 70% of *T. sirtalis* encountered were in grassy habitats, with most of the remainder associated with wetlands. Fitch (1965) found that *T. sirtalis* preferred relatively open habitats, including pond margins, meadows, fields, and edges of woodlands. Hart (1979) found *T. sirtalis* more in marsh habitat than pond habitat, and typically in areas with low moisture content. Charland and Gregory (1995) found that *T. sirtalis* showed a strong preference for areas with more overhead cover, and avoided open water, but also found that gravid females preferred warmer, rocky habitats. Burger *et al.* (2004) found that *T. sirtalis* in a riparian habitat showed a preference for basking in open areas on the ground rather than on branches or logs. Gregory (1984) found that *T. sirtalis* in coastal British Columbia were only found at sites that were dominated by freshwater rather than saltwater. Our work with *T. sirtalis* in eastern Ontario and western Quebec (Halliday and Blouin-Demers 2015, 2016, 2017; Halliday *et al.* 2015) demonstrated a density-independent preference for field over forest habitat, likely because fields have more optimal temperatures than forests, which lead to higher fitness (Halliday and Blouin-Demers 2016).

We conducted this study partly because eastern Ontario is a part of the range of *T. sirtalis* that is underrepresented in the literature. Studying habitat use by free-ranging *T. sirtalis* in open habitats expands on our previous work studying habitat selection between field

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and forest habitats in large enclosures (Halliday and Blouin-Demers 2015, 2016; Halliday *et al.* 2015). Our main goal was to test two competing, but not mutually exclusive, hypotheses: (1) habitat selection by gartersnakes is driven by frog abundance and (2) habitat selection by gartersnakes is driven by the need to thermoregulate. More specifically, we first wanted to determine if habitat use by *T. sirtalis* was related to frog abundance in different habitats and we predicted that gartersnakes should be more abundant where frogs are more abundant. Food is often considered a very important aspect of habitat quality (Kennedy and Gray 1993), but this might not be the case for snakes because most eat large meals infrequently (Shine 1986). Yet some studies with snakes have suggested that habitat use may be driven by food abundance (Robertson and Weatherhead 1992). Habitat quality for snakes is often linked to structural characteristics of habitats that allow them to thermoregulate or to hide (Blouin-Demers and Weatherhead 2001; Halliday and Blouin-Demers 2015, 2016). Therefore, we also wanted to determine if habitat use by *T. sirtalis* was related to structural characteristics of the different habitats, and we predicted that gartersnakes should be more abundant in more open habitats because these have higher thermal quality in temperate regions (Blouin-Demers and Weatherhead 2001; Row and Blouin-Demers 2006; Halliday and Blouin-Demers 2016).

Methods

Study site and data collection

In June 2014, we set up six study grids in the Stony Swamp sector of the National Capital Greenbelt in Ottawa, Ontario (45.283°N, 75.817°W; Figure 1). Vegetation characteristics were variable both among and within grids, varying from cattail (*Typha* sp.) dominated to mixes of shrub, grass, and forb. Each study grid was 100 × 100 m and we separated each grid into 25, 10 × 10 m sectors, marking the corners of each sector with bamboo poles marked with flagging tape. We placed a 60 × 60 cm cover object in the centre of each sector on substrate without standing water. In general, cover objects are a useful tool to monitor snakes (Halliday and Blouin-Demers 2015; Retamal Diaz and Blouin-Demers 2017). Cover objects were made of either tin (12 of 25 sectors) or plywood (13 of 25 sectors), which have been shown to be equally effective to sample small snakes in our area (Retamal Diaz and Blouin-Demers 2017).

We monitored each grid up to six times per year, but no more than once per week, between June and August of 2014 and 2015. More specifically, we visited grids 1 and 2 six times, grid 6 eight times, grids 3 and 5 nine times, and grid 4 ten times. When monitoring a grid, three to four people walked back and forth across the grid with an even spacing (~2 m between individuals) and at a constant pace. While searching for snakes and frogs, we looked under each cover object once during each survey, carefully looked in and around natural cover objects such as coarse woody debris without disturbing the habitat, and looked in the dense vegetation. When we detected a snake (either under a cover object or in the open), we worked together to capture the snake by hand. After catching each snake, we marked its ventral scales with a unique code using a medical cautery unit (see method and rationale in Winne *et al.* 2006). We also determined the sex of each snake and measured its snout-vent length and mass. We recorded which grid and sector the snake was caught in and released each snake at its point of capture. While monitoring each grid, we also counted the number of frogs (identified to species) encountered in each sector of each grid as a metric of food abundance; frogs are one of the main food sources for *T. sirtalis* (reviewed in Halliday 2016).

We characterized the habitat features in each sector of each grid based on the dominant vegetation class (cattail, dominant tree species, fern, forb, grass, horsetail, shrub), maximum height of vegetation, percent of sector covered by standing water, and maximum depth of water in the sector. We recorded up to two dominant vegetation classes in each sector if the vegetation was mixed.

Analyses

We tallied the number of snakes and frogs of each species encountered in each sector of each grid during each year of our study. For snakes, this tally is the number of individuals in each sector, while for frogs this tally is the number of frogs detected in each sector. We only had one recapture of a snake in the same sector, and we only counted that individual once within that sector. We encountered Common Gartersnake, Northern Watersnake (*Nerodia sipedon*), Red-bellied Snake (*Storeria occipitomaculata*), Eastern Milksnake (*Lampropeltis triangulum*), Green Frog (*Lithobates clamitans*), Northern Leopard Frog (*Lithobates pipiens*), Spring Peepers (*Pseudacris crucifer*), and a juvenile Eastern Newt (*Notophthalmus viridescens*); however, we encountered only enough *T. sirtalis* and *L. pipiens* for statistical analysis (Table 1). Despite our large array of cover objects, we only caught two *T. sirtalis* under covers, although we did catch all *S. occipitomaculata* and all *L. triangulum* under the covers.

We pooled *T. sirtalis* and *L. pipiens* abundances across surveys and converted each into a binary presence/absence variable of a species in each sector of each grid during each year. We then analyzed the presence/absence of *T. sirtalis* and *L. pipiens* within a sector using general linear mixed effects models with a binomial distribution in R (package lme4; function glmer; Bates *et al.* 2015). We built models with different combinations of the following fixed effects: presence/absence of each vegetation class, vegetation height, percent water, water depth, presence/absence of *L. pipiens* (only for the analysis of *T. sirtalis*), and year. We used grid ID as a random effect in all models. We compared models with different fixed effects using Akaike Information

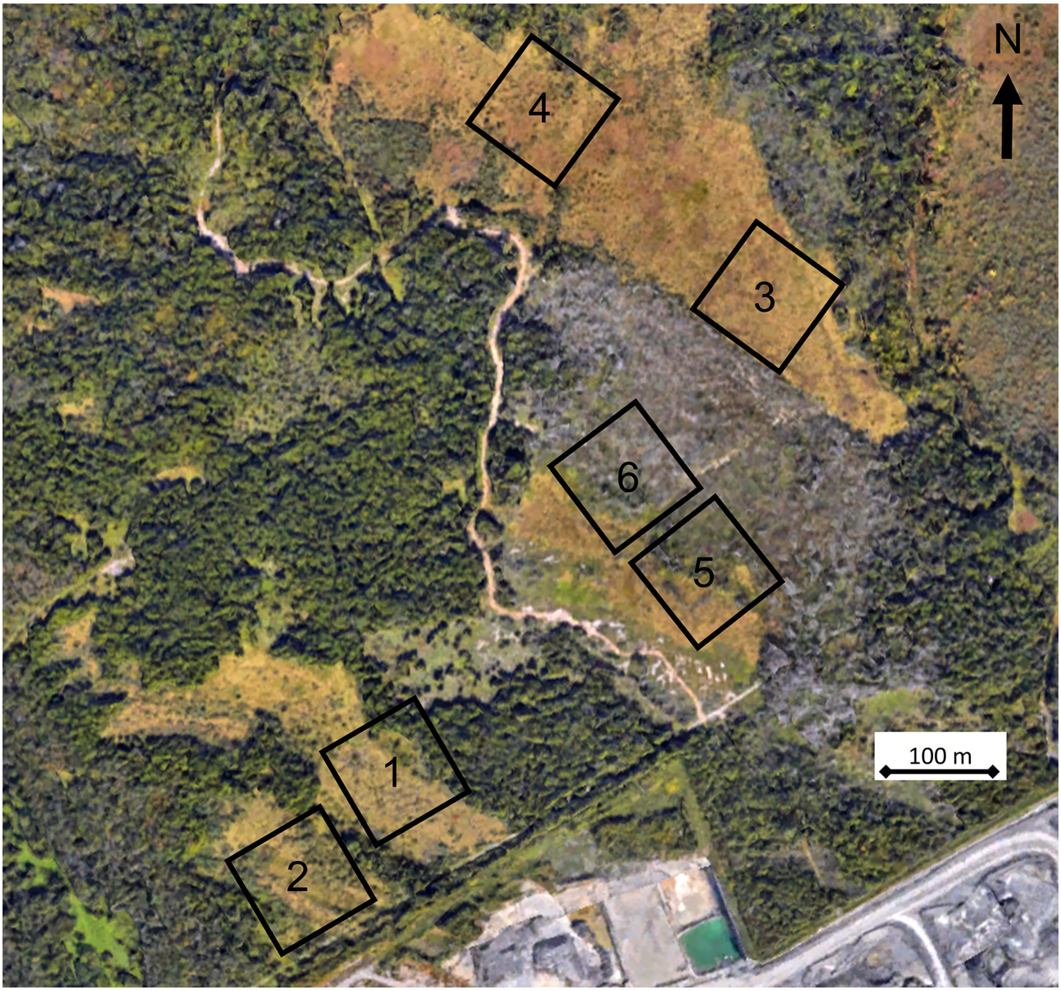

FIGURE 1. Layout of grids at study site in eastern Ontario, Canada. Map data © Google Canada.

TABLE 1. Abundance of snakes and amphibians encountered (number of unique individuals for snakes, but not necessarily for amphibians) in each year of a habitat selection study in six, 1-ha study grids near Ottawa, Ontario in 2014 and 2015.

Scientific name	Common name	2014	2015
Lampropeltis triangulum	Eastern Milksnake	1	1
Nerodia sipedon	Northern Watersnake	2	1
Storeria occipitomaculata	Red-bellied Snake	9	2
Thamnophis sirtalis	Common Gartersnake	20	36
Lithobates clamitans	Green Frog	7	4
Lithobates pipiens	Northern Leopard Frog	142	18
Notophthalmus viridescens	Eastern Newt	1	0
Pseudacris crucifers	Spring Peeper	3	7

Criterion (AIC; package stats; function AIC; R Core Team 2016) and selected the model with the lowest AIC as the final model; we considered models within 2 AIC units of the best model to be competing models and used model averaging to determine effect size (Burnham and Anderson 2002). We conducted all analyses in R version 3.3.0 (R Core Team 2016).

We conducted a second analysis of the abundance of both *T. sirtalis* and *L. pipiens* based on the total number of individuals encountered on each grid during each survey. For this analysis, abundance is the number of unique *T. sirtalis* encountered. This is likely also the number of unique *L. pipiens* counted because our unit of replication is a single survey event in a grid where it is highly unlikely that we would count the same frog twice. We used general linear models with a Poisson distribution (package stats; function glm) with the abundance of *T. sirtalis* or *L. pipiens* as the dependent variable and with year and grid identification as the independent variables. In the analysis of *T. sirtalis*, we also included the abundance of *L. pipiens* as an additional independent variable. We used bias-corrected Akaike Information Criterion (AICc; package qpcR; function AICc; Spiess 2014) to compare models for this analysis due to low sample size.

Finally, we compared the use of different vegetation types by *T. sirtalis* and *L. pipiens* to the availability of those vegetation types based on the methods described in Johnson (1980). We summed the number of captures and observations of each species in each dominant vegetation type during each year, and calculated the proportion of observations in each vegetation type. We then summed the number of sectors across all study grids that contained each dominant vegetation type, and calculated a proportion. We then compared use versus availability data (transformed into percent) for each species in each vegetation type in each year using χ^2 analysis in R (package stats; function chisq.test).

Results

Thamnophis sirtalis was more likely to be encountered in sectors with forbs (log odds ratio: 0.87, $z = 2.04$, $P = 0.04$) and was less likely to be encountered in sectors with grass (log odds ratio = −0.78, $z = 2.04$, $P = 0.04$; Figure 2a, Table S1). The probability of presence of *T. sirtalis* was unaffected by all other vegetation classes. Two of our study grids (5 and 6) had significantly more *T. sirtalis* than the other four grids ($P < 0.01$; Figure 3a, Table S2). These grids had high forb coverage, medium shrub and grass coverage, low fern and cattail coverage, and were rebounding from a 2012 forest fire. *Thamnophis sirtalis* was also more abundant in 2015 than in 2014 ($z = 3.23$, $P < 0.01$). The probability of presence of *T. sirtalis* was unaffected by water coverage or depth or frog abundance. *Thamnophis sirtalis* was more likely to be found in habitats with forbs relative to their availability, and were less likely to be found in habitats with grass relative to their availability in both 2014 ($\chi^2_{12} = 76.06$, $P < 0.01$) and 2015 ($\chi^2_{12} = 44.78$, $P < 0.01$; Figure 1a, Table S3).

Lithobates pipiens was more likely to be encountered in 2014 than in 2015 (log odds ratio = −2.39, $z = 5.23$, $P < 0.01$; Table S4), but their presence was unaffected by all vegetation classes (Figure 2b, Table S4). Two of our study grids (5 and 6) again had significantly more *L. pipiens* than other grids (Figure 3b, Table S5). According to the use-availability analysis, *L. pipiens* used habitats with forbs more than expected based on their availability, and used habitats with shrubs much less than expected based on their availability in both 2014 ($\chi^2_{12} = 55.82$, $P < 0.01$) and 2015 ($\chi^2_{12} = 70.04$, $P < 0.01$; Figure 2b, Table S3).

Discussion

Our study demonstrates that vegetation structure is an important predictor of habitat selection by *T. sirtalis*, but *L. pipiens* abundance is not. These results support our second hypothesis (habitat selection for thermoregulation), but do not support our first hypothesis (habitat selection for food). Our previous work (Halliday and Blouin-Demers 2016) demonstrated the importance of vegetation structure and habitat selection for thermoregulation at a coarse scale, where gartersnakes used warm open field habitat much more than cool forested habitat. In this study, we demonstrate that *T. sirtalis* prefer certain types of open habitats at a finer spatial scale. Specifically, we found more *T. sirtalis* near forbs (i.e., flowering plants like clover and vetch) more than expected based on availability, and fewer in grassy habitat than expected based on availability. Areas with high coverage of forbs were typically quite dry and offered good sites for basking. This forb habitat was also most abundant in sites 5 and 6 and is unique in the area due to a recent forest fire (summer 2012). Sites 5 and 6 had many fallen cedar trees, which provided potential cover where snakes could hide, mixed with plenty of small open sites for basking. We were able to observe snakes under these fallen trees without disturbing the habitat because the trunks were kept elevated from the ground by remaining branches. Although our use versus availability analysis did show a common preference for forbs by both *T. sirtalis* and *L. pipiens*, our analysis examining the influence of *L. pipiens* on *T. sirtalis* habitat selection demonstrated that the abundance of *T. sirtalis* in both grids and sectors of grids was unrelated to the abundance of *L. pipiens*. The exact sectors within grids where frogs were found did not coincide with the sectors where we found snakes. This suggests that, at a fine scale, *T. sirtalis* are not more likely to be found in locations where *L. pipiens* is found, despite this apparent shared habitat preference.

We found no effect of *L. pipiens* abundance on *T. sirtalis* habitat use, but this may be due to the low abundance of frogs in 2015 (Table 1). Indeed, habitat selection by *L. pipiens* is strongly related to moisture content in the soil (Blomquist and Hunter 2009). Whereas 2014 was a very wet year, 2015 was a very dry year, which likely influenced the abundance of *L. pipiens* that we encountered on our grids. Although it has been suggested that habitat use by snakes might be linked to amphibian presence (Robertson and Weatherhead 1992), other evidence suggests that daily habitat use by snakes is not linked to food abundance because snakes generally eat infrequently and are not limited by food (Halliday and Blouin-Demers 2017). Long-term data with a much larger sample size would be required to truly test this hypothesis given the low abundance of snakes and the large fluctuations in frog abundance from year to year. Frogs are also just one food source for *T. sirtalis*; their second most consumed food is earthworms, and their third through fifth most consumed food items are sal-

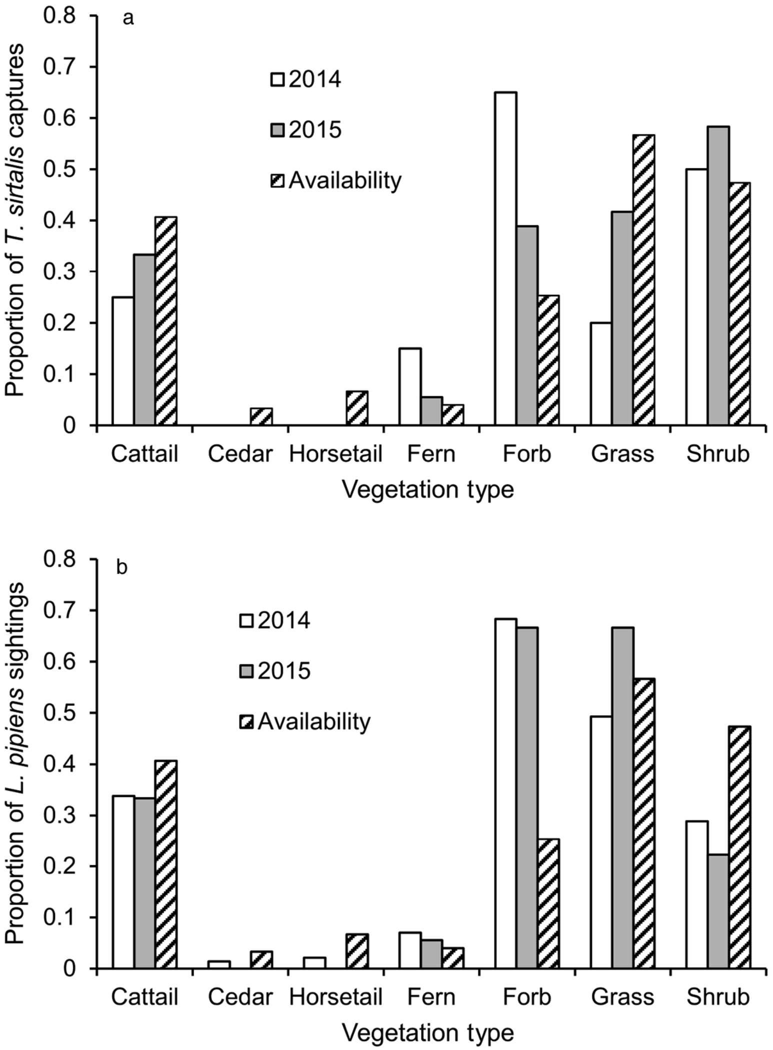

FIGURE 2. The proportion of captures of Common Gartersnakes (*Thamnophis sirtalis*; a) and sightings of Northern Leopard Frogs (*Lithobates pipiens*; b) in 1-ha study grids with different vegetation types in 2014 (white bars) and 2015 (grey bars) near Ottawa, Ontario, Canada. Hatched bars represent the proportion of sectors from all grids with each vegetation type (availability).

amanders, fishes, and small mammals (reviewed in Halliday 2016). Therefore, to truly test the hypothesis that food abundance is important in habitat selection, future studies should track the abundance of these other prey items in relation to the habitat selection of *T. sirtalis*. If *T. sirtalis* only spend a small amount of time hunting and eating prey, then the overall habitat selection that we observed would not reflect their choice for hunting. Radio-telemetry studies, along with detailed information on the activities being performed in different habitats, is crucial for understanding the reasons that *T. sirtalis* use different habitats.

The presence of water was not important to the habitat use of *T. sirtalis* in this study. This is despite water being important in previous habitat selection studies of *T. sirtalis* (Charland and Gregory 1995; Ernst and Ernst 2003), where they avoided deep water, but were still found in close proximity to water. Water levels in our study differed drastically in space and time. 2015 was a very dry year, and all of the water on a few grids completely disappeared by the end of August. In 2014, water levels remained high for the entire season. Given the few snake captures, this made it difficult to detect a water effect.

Detection probability of snakes and frogs likely differed between different vegetation classes. For instance, tall cattails limited our ability to detect snakes to within 2 m, whereas we could detect snakes farther away in

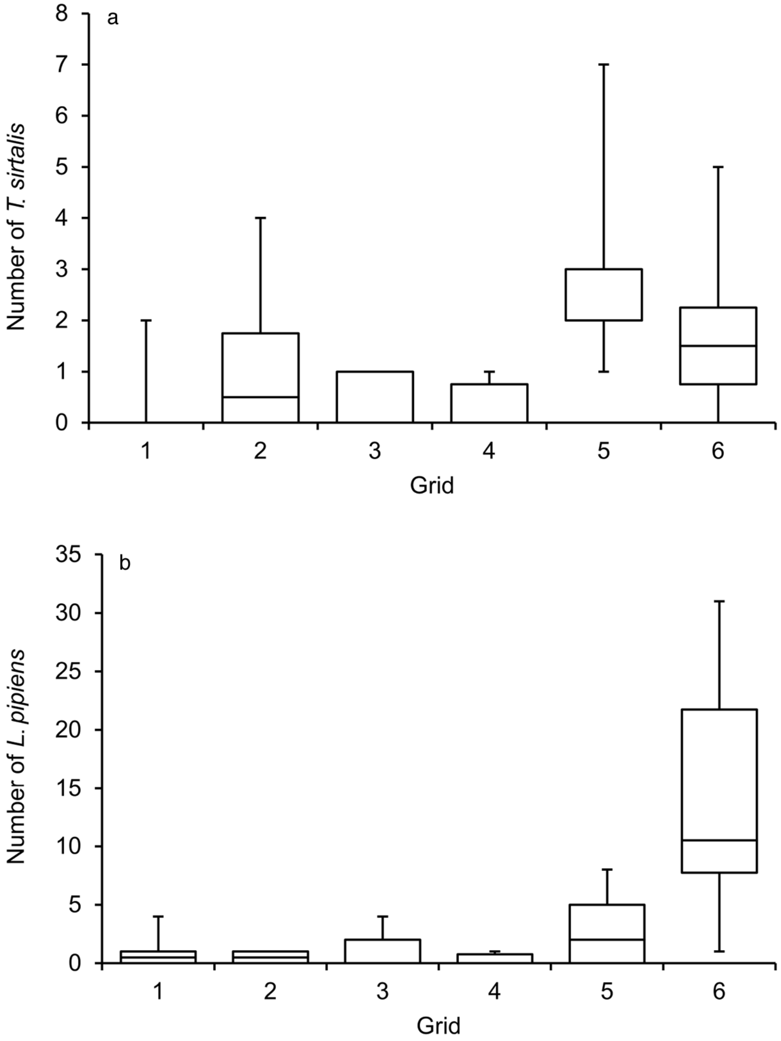

Figure 3. The number of Common Gartersnakes (*Thamnophis sirtalis*; a) and Northern Leopard Frogs (*Lithobates pipiens*; b) captured on each 1-ha study grid during each survey in 2014 and 2015 near Ottawa, Ontario, Canada. The line within the box is the median, the box represents the interquartile range, and the whiskers represent minimum and maximum values.

habitats with low vegetation. Snakes also effectively hid in tall grass, but tended to flee these areas when we approached, making it easier to detect them. It is therefore possible that this detection bias between habitats affected our results. However, regardless of habitat type, we kept a 2 m spacing between individuals for all surveys, and therefore did not rely on being able to detect snakes at long distances. Although this would not fully remove any potential bias, it should have helped to minimize detection bias between habitats. Future studies could use radio-telemetry to measure habitat selection by *T. sirtalis* in these habitats, and could also estimate observation bias by estimating the ability to visually find a radio-tagged snake in these habitats. Radio-telemetry also comes with its own biases, however, related to generally small sample sizes, limits on the size of snakes that can be studied, and issues related to implanting or affixing transmitters to snakes. We therefore recommend using data from a combination of methods, including visual surveys like ours and radio-telemetry.

In conclusion, vegetation structure is important to the habitat selection of *T. sirtalis*, likely because of its effect on microhabitat quality for activities like basking and hiding. *Lithobates pipiens* abundance and water cover were not important to the habitat selection of *T. sirtalis* in our study, but long-term data would be required to truly test the importance of these factors in habitat selection due to their high variance within and between years.

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SUPPLEMENTARY MATERIAL:

TABLE S1. Model selection and final model output for general linear mixed effects models examining the presence/absence of Common Gartersnakes (*Thamnophis sirtalis*; Ts) based on habitat features and the presence/absence or abundance of Northern Leopard Frogs (*Lithobates pipiens*; Lp).

TABLE S2. Model selection and final model output for general linear mixed effects models examining the abundance of Common Gartersnakes (*Thamnophis sirtalis*; Ts) in study grids over two years near Ottawa, Ontario, Canada.

TABLE S3. Habitat use versus habitat availability for Common Gartersnakes (*Thamnophis sirtalis*, top) and Northern Leopard Frogs (*Lithobates pipiens*, bottom) selecting habitats near Ottawa, Ontario, Canada.

TABLE S4. Model selection and final model output for general linear mixed effects models examining the presence/absence of Northern Leopard Frogs (*Lithobates pipiens*; Lp) based on different habitat features.

TABLE S5. Model selection and final model output for general linear mixed effects models examining the abundance of Northern Leopard Frogs (*Lithobates pipiens*; Lp) in different study grids over two years near Ottawa, Ontario, Canada.

First record of Eurasian Water-milfoil, *Myriophyllum spicatum*, for the Saint John River, New Brunswick

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Abstract

Eurasian Water-milfoil (*Myriophyllum spicatum* L.) is regarded by conservation practitioners as one of the most challenging invasive aquatic plants to manage. Owing to its broad tolerance to environmental conditions, vegetative propagation, and rapid establishment and growth, *M. spicatum* introductions have the potential to drastically alter macrophyte species assemblages via a loss of native species and their respective ecosystem functions. Following the discovery of a single specimen of *M. spicatum* in the Saint John River, near Fredericton, New Brunswick (Canada) we further investigated the localized distribution of this non-indigenous species. Thirteen areas were identified as potential *M. spicatum* habitat and were surveyed by wading or snorkeling. Specimens of *M. spicatum* were collected and morphological identifications were verified through genetic analyses (ITS2; *rbc*La). The results of our investigation confirm the presence of *M. spicatum* at six different locations within the Saint John River. Here we discuss the implications of this discovery in the context of the contiguous aquatic habitats along a large river system.

Key words: Eurasian Water-milfoil; *Myriophyllum spicatum*; aquatic invasive; Saint John River

Introduction

Approximately 15% of non-indigenous plant species become invasive causing irreversible disruptions to ecosystem functions (Westbrooks 1998). In aquatic environments, not only do invasive plants alter floristic assemblages via loss of native species (Aiken *et al*. 1979; Boylen *et al.* 1999) and their respective ecosystem functions (Duffy and Baltz 1998; Thomaz and da Cunha 2010) and compromise habitat for many other species, but they also alter environmental flows, nutrient cycling, and can directly influence water quality (Zedler and Kercher 2004; Kovalenko and Dibble 2010; Villamagna and Murphy 2010). Additionally, invasive aquatic plants often grow to high densities and are detrimental to the economic, recreational, and aesthetic qualities of waterways (Newroth 1985; Eiswerth *et al.* 2000). Mitigation of the negative impacts of aquatic introductions requires active control measures and is costly (Pimental *et al.* 2004).

One of the five most noxious aquatic plant invaders of aquatic ecosystems is Eurasian Water-milfoil (*Myriophyllum spicatum* L.; Cronk and Fennessy 2001). Native to Eurasia and northern Africa (Sennikov 2016), *M. spicatum* is now present on every continent except Antarctica (Cook 1985). While the impacts of the introduction of *M. spicatum* vary in magnitude among different aquatic environments and in different regions (Smith and Barko 1990), it is generally acknowledged among scientists and conservation practitioners that this species frequently establishes dense, monospecific beds that outcompete local flora and reduce the diversity and abundance of native species (Grace and Wetzel 1978; Madsen *et al.* 1991; Boylen *et al.* 1999). In some instances, this species has outcompeted native flora in as little as 2–3 years (Aiken *et al.* 1979; Newroth 1985; Boylen *et al.* 1999). Considered the most widely managed invasive aquatic plant in the United States (Bartodziej and Ludlow 1998), *M. spicatum* is on several regional invasive species watch lists and is listed as one of the ten most unwanted species in Maine, USA (Hill and Williams 2007), and New Brunswick, Canada (New Brunswick Alliance of Lake Associations website: http://www.nbala.ca/new-page-1).

The vector and timing of introduction of *M. spicatum* to North America is not completely understood. While Couch and Nelson (1985) suggest *M. spicatum* was introduced to North America in the 1940s, Reed (1977) reviewed historical herbarium specimens and provided evidence that the earliest verified records of *M. spicatum* from North America are dated back to at least 1881 but acknowledged that the introduction was possibly as early as 1848. It is not uncommon for non-indigenous species to exhibit an initial lag in their growth before they become invasive, and many non-indigenous aquatic plant introductions go unnoticed until they are established as truly invasive. Thus, it is highly probable that *M. spicatum* was present in North America as early as 1848 and Couch and Nelson's (1985) report regarding introduction in the 1940s more accurately reflects the timing at which this species was first observed as invasive.

In an assessment of historical records for the distribution of *M. spicatum* in North America, Reed (1977) also observed a disjunct distribution with populations in eastern North America, southeastern North America, and an isolated region in California. He attributed this disjunction to independent introductions that were most likely a consequence of the release of aquarium plants, as various species of *Myriophyllum* were commonly cultured and distributed for the aquarium trade at this time (Reed 1977). While the release of aquarium plants may be the original source of introduction events across North America, introduction to new waters is now primarily attributed to fragments introduced by boats and their associated trailers (Johnson *et al.* 2001; Rothlisberger *et al.* 2010).

Successful eradication of recently established invasive species populations is highly dependent on rapid detection and prompt management actions (Willby 2007). Two factors may hinder the rapid detection of *M. spicatum*: difficulty in detection because it is primarily beneath the water's surface and difficulty in identification versus similar native congeners (especially the sister species Siberian Water-milfoil, *M. sibiricum* Komarov) because the key morphological features vary with phenotypic plasticity (Strand and Weisner 2001) and/or hybridization (Sturtevant *et al.* 2009).

While conducting macrophyte surveys for 171 sites along the Saint John River (SJR) as a part of a larger aquatic ecosystem study, the Mactaquac Aquatic Ecosystem Study (http://canadianriversinstitute.com/research/mactaquac-aquatic-ecosystem-study/), we discovered a single inconspicuous specimen of *M. spicatum*. Prior to our discovery of this species in the SJR, Hinds (2000) reported that this species had been collected from a small pond in Fundy National Park (Hinds 2000: 667). The introduction of *M. spicatum* to the SJR poses a threat to the submerged aquatic flora within the river and associated waterways. To assess the local distribution of this non-indigenous species, we used an active survey approach that involved snorkelling surveys of potential habitat and molecular approaches (DNA analyses) to verify our taxonomic identifications.

Methods

To identify potential *M. spicatum* habitat for this survey we looked for areas in the Fredericton region of the SJR (where the first specimen was initially collected) that were consistent with habitat conditions reported for this species (Aiken *et al.* 1979). Our survey emphasized sheltered cove environments or other low flow areas with soft substrate, as well as areas with frequent boat traffic (Figure 1). Where necessary, snorkelling surveys were conducted to ensure we could observe the submerged flora.

Apical portions of plants morphologically identified in the field as *M. spicatum* were collected and preserved as herbarium vouchers stored at the Connell Memorial Herbarium (UNB IH) at the University of New Brunswick (Table 1). Leaf tissue sub-samples were dehydrated in silica for subsequent genetic analyses (Fazekas *et al.* 2012). Dehydrated tissue was sent to the Canadian Centre for DNA Barcoding (CCDB) for DNA extraction, PCR amplification, and sequencing according to CCDB standardized protocols (Fazekas *et al.* 2012). To facilitate comparison of our genetic results with taxonomic data available in GenBank (NCBI Resource Coordinators 2016) and the Barcoding of Life Data System (Ratnasingham and Hebert 2007) we selected two standard land plant DNA barcode markers, *rbc*La and ITS2 (Fazekas *et al.* 2012).

Results and Discussion

Analyses of ITS2 and *rbc*La sequence data was consistent with the morphological-based identification of *M. spicatum* at six of 13 sites surveyed (Table 1). Four of the six sites where *M. spicatum* is present had only a few scattered plants (Table 1). The remaining two sites where this species was found had patches where it was clearly established as dense macrophyte beds (Figure 2). To assess the potential future impact of this introduction on the native aquatic flora, we reviewed what has been reported for the biology of this invasive species and considered what risks this may present for the aquatic environments along the SJR.

Reproduction

Myriophyllum spicatum shoots emerge and exhibit rapid growth from an overwintering rhizomatous mass in the early spring and throughout summer. As the growing season progresses, plant growth peaks at the water surface where stems are highly branched forming dense floating canopy (Titus *et al.* 1975). Vegetative portions of the plants break off throughout the growing season and in the fall when plants typically die back to the propagating rhizome crowns (Aiken *et al.* 1979).

Fragmented vegetative portions are the primary mode of reproduction and spread for *M. spicatum* within an aquatic ecosystem (Kimbel 1982). In the SJR, downstream spread of this species via vegetative fragmentation is naturally facilitated by peaks in hydrological flows, as well as seasonal ice scouring. The spread of *M. spicatum* between watersheds is largely attributed to vegetative material transported by boat motors and trailers (Johnson *et al.* 2001; Rothlisberger *et al.* 2010). In the Fredericton region of the SJR where we have confirmed the presence of *M. spicatum*, further spread by boat motors is a concern as this area is frequently used by recreational boaters. Consequently, this increases the potential of the species to move in larger, discontinuous jumps, enabling the species to spread upstream and to new water bodies.

Like many successful invasive species, *M. spicatum* has multiple modes of reproduction and frequently exhibits sexual reproduction in addition to vegetative fragmentation. Perhaps more concerning than the ability to undergo both asexual and sexual reproduction, is the ability of *M. spicatum* to hybridize with its native sister species *M. sibiricum* to produce plants that exhibit "hybrid vigor"—plants with competitive phenotypes that are superior to both parent species (Moody and Les 2002, 2007; Sturtevant *et al.* 2009). This hybridization, between an introduced invasive species and a native

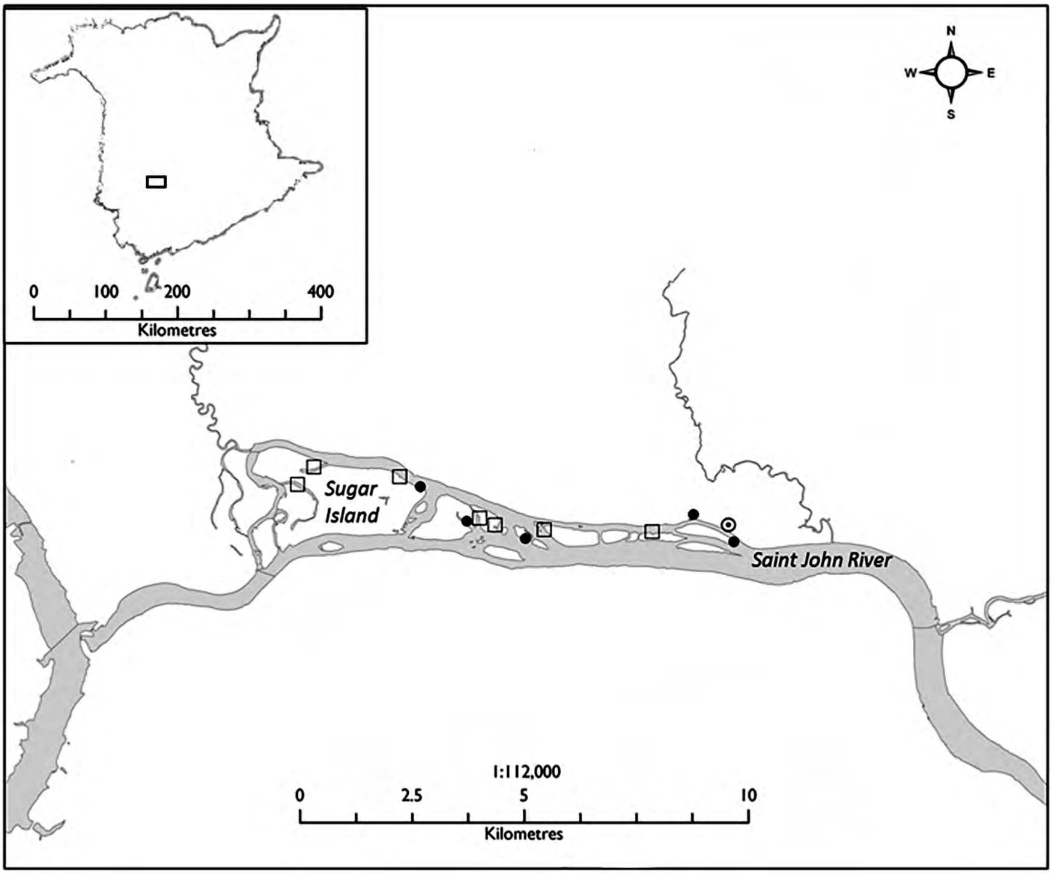

FIGURE 1. Six sites within the Fredericton region of the Saint John River where specimens of Eurasian Water-milfoil (*Myriophyllum spicatum*) were collected and identified (denoted by "●"). ⊙ = original site of collection; □ = potential *M. spicatum* habitat investigated but species was not present.

species, can result in "genetic pollution" introducing new alleles to the population and potentially wiping out locally adapted genotypes (Laikre *et al.* 2009). In New Brunswick, the native species *M. sibiricum* is classified as potentially vulnerable (S3/S4) and is widespread on the lower SJR system (S. Blaney pers. comm. February 2015). Thus, the ecological risks posed by the potential hybridization of *M. spicatum* and *M. sibiricum* are two-fold: hybridization may give rise to populations the exhibit hybrid-vigor and promote further colonization and populations of the native species, *M. sibiricum*, may be put at risk due to genetic pollution or competition pressure with *M. spicatum* or *M. spicatum* × *M. sibiricum* hybrids.

Habitat and area for potential colonization

Most commonly establishing in water with depth ranging 1–3 m, *M. spicatum* has been reported as deep as 10 m (Aiken *et al.* 1979), reaching 7 m high. Plants thrive in eutrophic lakes with soft organic substrates but persist in a wide range of substrates and environmental conditions (Nichols and Shaw 1986). With regard to water quality, *M. spicatum* is able to persist in a wide pH range (5.4–11), tolerate salinity up to 15 ppt, and tolerate various industrial pollutants (Aiken *et al.* 1979; Wang *et al.* 1996). When growing in shallow areas susceptible to drops in water level that may leave it exposed, *M. spicatum* assumes a terrestrial form allowing it to gradually become stranded and survive (Aiken *et al.* 1979). The broad environmental tolerance in this species enables it to colonize various types of lakes, wetlands and salt marshes, or river margins, coves, and inner island channels as observed in our surveys. Downstream of our confirmed *M. spicatum* population is approximately 130 km of river with extensive seasonal flood plain and contiguous habitat that has high potential for colonization by this species.

The Grand Lake Meadows (GLM), located approximately 40 km downstream from the sites of the *M. spicatum* occurrence, is the largest freshwater wetland and floodplain in New Brunswick. It includes the provincial Grand Lake Class II Protected Natural Area (GL PNA). Recent surveys of the flora in the area report 98 rare species that contribute 20% of the total flora (Papoulias *et al.* 2006). One of the taxa reported, Budding

TABLE 1. Eurasian Water-milfoil (*Myriophyllum spicatum*) specimens and associated collection and GenBank records.

UNB IH accession (research specimen number)	Collectors	Location	Collection date	Habitat	Abundance	GenBank accession number	
						ITS 2	*rbc*La
66290 (MRB000031)	M. Bruce C. Brooks Z. Compson S. Andrews	45.97577°N, 66.68854°W	20 August 2015	Edge of back channel, soft bottom, water ~60 cm at time of collection	Single small plant	MG648683	MG648689
66921 (MRB000034)	M. Bruce H. Johnson G. Filloramo	45.97711°N, 66.69473°W	4 July 2016	Sheltered, soft substrate	Dense patch (~4 m × 5 m) surrounded by several peripheral plants	MG648684	MG648690
66292 (MRB000035)	M. Bruce S. Andrews	45.97552°N, 66.75940°W	16 July 2016	Sheltered island inlet, soft substrate, water ~120 cm at time of collection	Numerous scattered plants	MG648686	MG648692
66293 (MRB000036)	M. Bruce H. Johnson G. Filloramo	45.98299°N, 66.77400°W	16 July 2016	Sheltered island inlet, soft substrate, water ~180 cm at time of collection	Dense patch in center of cove, ~2 m × 3 m	MG648685	MG648691
66293 (MRB000037)	M. Bruce B. Pardy	45.972010°N, 66.68262°W	4 July 2016	Small cove on back channel, soft substrate, water ~90 cm at tie of collection	A few plants	MG648687	MG648693
66294 MRB000039	M. Bruce S. Andrews Z. Compson	45.97290°N, 66.74338°W	4 September 2015	Edge of island, mixed substrate, water ~60 cm at time of collection	Single small plant	MG648688	MG648694

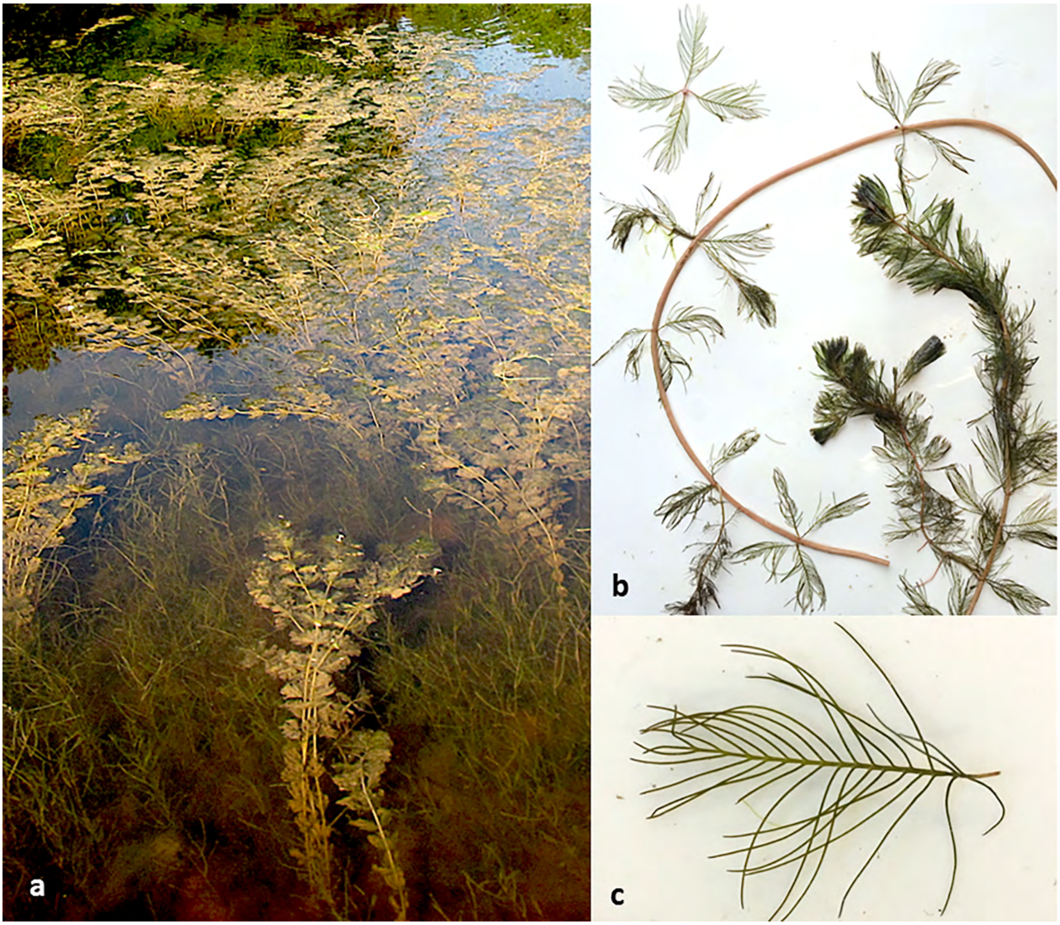

FIGURE 2. Eurasian Water-milfoil (*Myriophyllum spicatum*). a. Overall habit, plants growing in a dense patch with a high degree of branching, forming a canopy at the water surface. b. Specimen of *M. spicatum* showing leaves in whorls of four along stem. c. Single pectinate leaf with 15 pairs of pinnae. Photos: M. Bruce.

Pondweed, *Potamogeton berchtoldii* subsp. *gemmiparus* (J.W. Robbins) Les & Tippery, is the only known record of this species for New Brunswick and it is rare on the national level (Papoulias *et al.* 2006). In the spring, the SJR floodplain spills into the GLM and GL PNA, downstream of our confirmed populations of *M. spicatum*. The GLM and the GL PNA is thus an area of special concern that should be monitored for a potential M. *spicatum* invasion.

Options for controlling further spread

Early detection of *M. spicatum* and minimizing risk of further spread of early introductions hold the most promise for aquatic ecosystem management (Willby 2007). For individual plants, or small stands of *M. spicatum*, shading with a black cloth that inhibits photosynthesis can kill the plants (Bailey and Calhoun 2008). This could be an option for the plants that were found in this study, or small isolate populations in other areas. Another option that may be useful (for at least this area of the SJR) is to reduce water flow when air temperatures drop to freezing in early winter. Exposing the crown of the plant to freezing temperatures has shown some success in managing populations of this species in other areas (Bates and Smith 1994; Wagner *et al.* 2008). Considering that our observed plants were all in shallow areas below the Mactaquac Hydrogeneration Station (MGS) which have been observed to be exposed at times when the MGS retains water (M.B. pers. obs. early August 2015 and 2017), this could be an option for managing the small populations in this area. Where *M. spicatum* has established as invasive, raking of vegetation helps to temporarily reduce biovolume; however, reproductive fragments render application of this method as high-risk for further spread. Herbicides and the introduction of natural pests have also shown some promise, although the previous studies do not assess potential negative impacts to non-target native species within the aquatic ecosystem (Creed 1998; Cock *et al.* 2008).

Conclusions and future investigations

With knowledge of the presence of this non-indigenous species within the SJR, we intend to quantitatively assess the amount of potential downstream habitats available for colonization by developing spatial models of potential habitat. Spatial models have been used in a number of ecological and biological studies to identify links between the abiotic and biotic environment (e.g., Milhous *et al.* 1981; Milhous 1999). Such models use environmental variables, such as velocity, substrate composition, temperature, etc., to explain the presence and spatial distribution of biota of interest (e.g., Dunbar *et al.* 2011). We intend to build a spatial model to (a) identify habitat utilized by *M. spicatum* and (b) apply our model to the SJR to identify areas that may potentially be available for colonization.

Unfortunately, we currently cannot ascertain when or how this species arrived, or the full extent of this species' range in the SJR. Our immediate priority is to extend our survey coverage and to determine if *M. spicatum* is present beyond the range we have observed. Prior to the recreational boating season, we will engage local conservation practitioners and develop an action plan to educate and engage the public as to the presence of *M. spicatum* in this region in an effort to minimize the further spread of this species and mitigate the negative effects of already established occurrences.

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Manitoba's endangered alvars: an initial description of their extent and status

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Abstract

Alvars are rare in Canada and uncommon globally. This study represents the first formal attempt to describe and delineate the extent of alvars in Manitoba. A systematic examination of the Interlake region's edaphic and biological characteristics, using a geographic information system, resulted in the identification of 67 sites warranting further field study. Of these sites, 61 were surveyed and information was collected on vegetation composition and structure, soil characteristics, land ownership, and land use. Alvar was confirmed at 28 sites, extending over approximately 3930 ha in five geographically distinct clusters. Four putative types of alvar communities are described: grassland, shrubland, savannah, and wetland. Livestock grazing is the dominant land use and occurs across more than three-quarters of Manitoba alvar. Approximately 12% coincide with mining claims or quarry leases. Two-thirds occur on publicly owned land.

Key words: Alvar; karst; endangered ecosystem; Manitoba; Interlake; limestone; dolomite

Introduction

Alvars are globally uncommon ecosystems that are distinctive for their unusual plant species composition and associations and natural openness in otherwise forested regions (Catling and Brownell 1995; Reshcke *et al.* 1999), although alvar woodlands and the associated successional stages are also important components (Catling and Brownell 1999a; Catling *et al.* 2002; Brunton and Catling 2017). Alvars have thin or absent soils underlain by flat limestone or dolomitic bedrock that restricts drainage; thus, they are subject to extreme variations in moisture availability that range from drought conditions to periodic flooding (Brunton 1988; Catling and Brownell 1995; Reschke *et al.* 1999; Catling 2009a). The physical structure and species composition of alvar plant communities can vary; Great Lakes alvars, for example, have been differentiated into 13 types (Reschke *et al.* 1999). In Manitoba, alvar-like ecosystems that support species characteristic of both prairie and boreal forest, with a limited occurrence of trees and occasional exposure of dolomitic pavement, have been described (Hamel and Foster 2004).

In Canada, alvars are found in the Great Lakes region, Quebec (Reschke *et al.* 1999), and the Northwest Territories (Catling 2009a). The presence of alvar in Manitoba was noted by Catling (2009a), but no information on its extent was provided. Although the precise extent of alvars in North America is not yet known, their distribution is fragmented and loosely follows the edge of the Canadian Shield where postglacial meltwaters have exposed limestone bedrock (Catling 2009a). Before our study, alvar-like ecosystems associated with near-surface dolomitic limestone pavement and inland cliffs had been documented at five locations in Manitoba between the southern basins of Lakes Manitoba and Winnipeg, i.e., the Interlake region (Hamel and Foster 2004). In 2011, an Ontario alvar expert (John Riley) accompanied us to one of these locations and confirmed that the ecosystem shared characteristics consistent with alvar ecosystems in Ontario and were worthy of further study and formal description.

In 2015, the Manitoba government listed alvar as endangered under the Manitoba *Endangered Species and Ecosystems Act* using the authors' unpublished information to support determination of its conservation status.

The results of this study were previously published in a technical report (Manitoba Alvar Initiative 2012). This paper refines those results and confirms the findings in the context of the established body of knowledge on North American alvars. The objectives of this study were to survey and map alvars in the Interlake region of Manitoba; to describe their physical structure and species composition; and to determine land ownership and land uses of Manitoba alvars.

Methods

We used a geographic information system (GIS) to identify and delineate 67 sites of potential alvar encompassing 6313 ha (Figure 1) in the south Interlake and adjacent regions. We examined spatial data layers of geomorphologic and vegetative features representative of alvar-like sites identified by Hamel and Foster (2004). Layers included orthophotographs (to assess vegetation cover), soil classification data (to determine soil depth and the presence of near-surface limestone bedrock), and a digital elevation model (to identify the location of ridges; Manitoba Conservation and Water

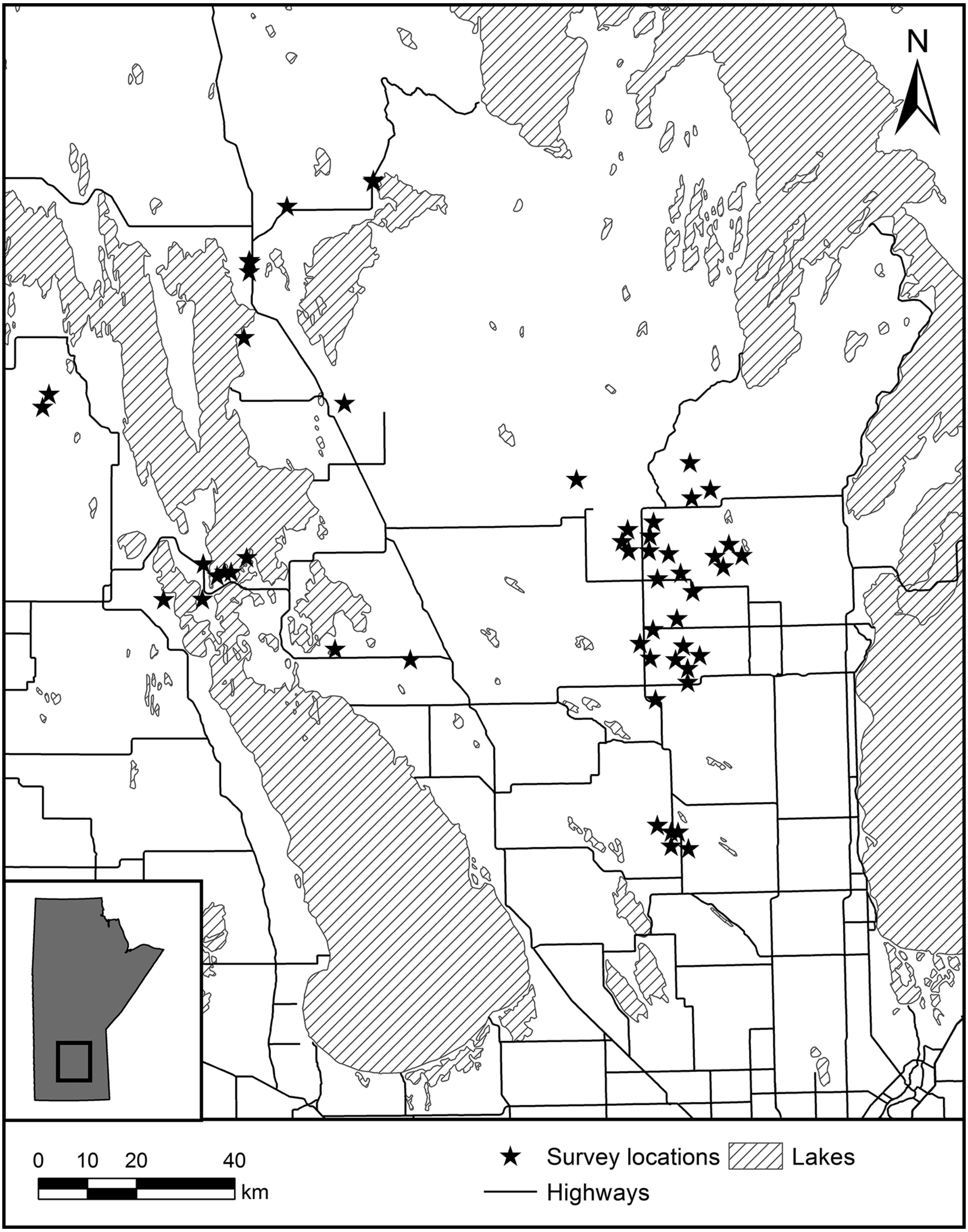

FIGURE 1. Survey locations (stars) were considered potential locations for alvar based on similarities in geological and soil characteristics to previously confirmed communities in Manitoba.

Stewardship 2012a). Between June and August 2012, we surveyed and assessed 61 sites to determine whether they supported alvar. We attempted to visit all potential sites regardless of ownership, but we did not receive permission to access six private land parcels.

A site was determined to be alvar if it met the following criteria: presence of flat limestone or dolomite bedrock that restricts drainage; soil thin—with a depth up to 15 cm that is not the result of mechanical removal—or absent (criterion used by Brunton 1988; Catling and Brownell 1995; Reschke *et al.* 1999); and tree canopy cover <60% (criterion used by Reschke *et al.* 1999). Although alvars can occur on soil deeper than 15 cm (Reschke *et al.* 1999), such sites were not included in the estimation of extent for this study because they could not be confirmed as being alvars without more detailed analyses of the species composition and/or investigation of other ecologically distinct characteristics resulting from the influence of an underlying bedrock pavement.

If not visible at the surface, limestone pavement was detected by digging small test holes. We determined soil depth by pressing a metal rod into the soil and measuring depth at impact with bedrock. Evidence of extreme moisture variability was based on observations of standing water following rain events, the presence of algae on dry pavement, thin bare soil (without evidence of disturbance), and restricted vegetation and lichen growth patterns. We recorded qualitative observations of the dominant plant species, soil depth, unique topographic features, land use, and patterns of flooding, drought, and drainage.

The potential extent of alvar at each survey site was mapped as polygons in GIS. Boundaries were delineated by using ground-truthed global positioning system coordinates and interpreting orthophotographs. These maps indicate the estimated maximum extent of the alvar communities observed. Within mapped habitat patches, there may be areas without alvar, or an area may represent a mosaic of alvar and other ecosystems.

Dominant physiognomic characteristics were used to categorize alvars into types to better describe the variation observed. Alvar types were characterized first by growth form (tree, shrub, forb, or graminoid), then vertical structure (<10% tree canopy or 10–60% tree canopy, comparable to thresholds used to distinguish savannah from other upland ecosystems found in the Interlake region; Minnesota Department of Natural Resources 2005), and, finally, by wetland or upland species affinities. Putative descriptions of each type's composition and variation were prepared using the data collected during site surveys. We used vegetation survey plots at a small sample of sites to supplement the general survey data and test the accuracy of these descriptions. Nine 20 m × 50 m plots, distributed among four sites, were randomly placed in what appeared to be unique subtypes of alvar. Each plot was divided into six subplots: one 20 m × 20 m; four 10 m × 10 m; and one 20 m × 10 m. The canopy cover of vascular plants, bryophytes, and lichens was recorded by visual observation within the four 10 m × 10 m subplots using the following cover classes: <0.1%, 0.1 to <1%, 1 to <2%, 2 to <5%, 5 to <10%, 10 to <25%, 25 to <50%, 75 to <95% and ≥95%. The additional two plots were used to capture the cover class of any species not recorded in the initial four plots. Soil depth was recorded on the centre line and at 10 m and 30 m along the plot starting from the 10 m × 20 m end. Voucher specimens obtained for vascular plants, bryophytes, and lichens were deposited in the University of Manitoba herbarium (WIN). A statistical analysis was not completed.

The bedrock composition of the limestone underlying alvar was compared at each site by overlaying the mapped alvar polygons with a GIS shapefile of the geological periods of bedrock formation (Manitoba Mineral Resources 2012a) to identify patterns related to alvar type and distribution.

Results and Discussion

Extent and distribution

Alvar was found at 28 of the 61 survey locations, with a maximum extent of ~3934 ha. Alvars >16 ha often supported internal patches of non-alvar ecosystems, such as forest or prairie, where soil depth was greater than 15 cm.

We mapped 101 spatially distinct units of alvar, varying from 0.4 ha to 809 ha and grouped these units into five geographically distinct sites (Figure 2). The Marble Ridge Alvar, referred to as Marble Ridge A, B, and C Alvars, follows a limestone formation of the same name, along which inland limestone cliffs are also found. The Peguis Alvar is immediately east of the Peguis First Nation Reserve, and the Sylvan Alvar is almost completely within the boundaries of the Sylvan Dale Community Pasture. The Poplarfield Alvar represents a group of small, isolated units near Poplarfield. The Clematis Alvar is located in and around the Clematis and Sandridge Wildlife Management Areas.

Alvar types

Alvars were categorized into four putative types: grassland (graminoid dominated, <10% tree cover, upland affinity), shrubland (shrub dominated, <10% tree cover, upland affinity), savannah (shrub dominated, >10% tree cover, upland affinity), and wetland (graminoid dominated, <10% tree cover, wetland affinity). Many sites supported multiple types of alvar occurring in combination. A list of plant and lichen species observed in each alvar type is shown in Table 1, but quantitative values are not presented as the plot data are not fully representative of the variation that exists within the types described.

Grassland alvars have nearly continuous vegetative cover, with soil depth typically ranging from 5 cm to 10 cm, and only occasional patches of limestone pavement (Figure 3). They are dominated by upland graminoid species, with high forb and low shrub cover. Trees are typically absent or restricted to the periphery. Moss provides significant ground cover among and beneath other vegetation. Bare soil, exposed limestone, and bryophyte and lichen growth directly on the limestone pavement were uncommon. These sites are generally flat, although some areas have small (typically <1 m in height) outcrops along the edges of plateau formations. We observed less evidence of flooding following rain compared with other alvars, although drainage is restricted and water pools on the limestone pavement. We did not observe conditions immediately following spring melt.

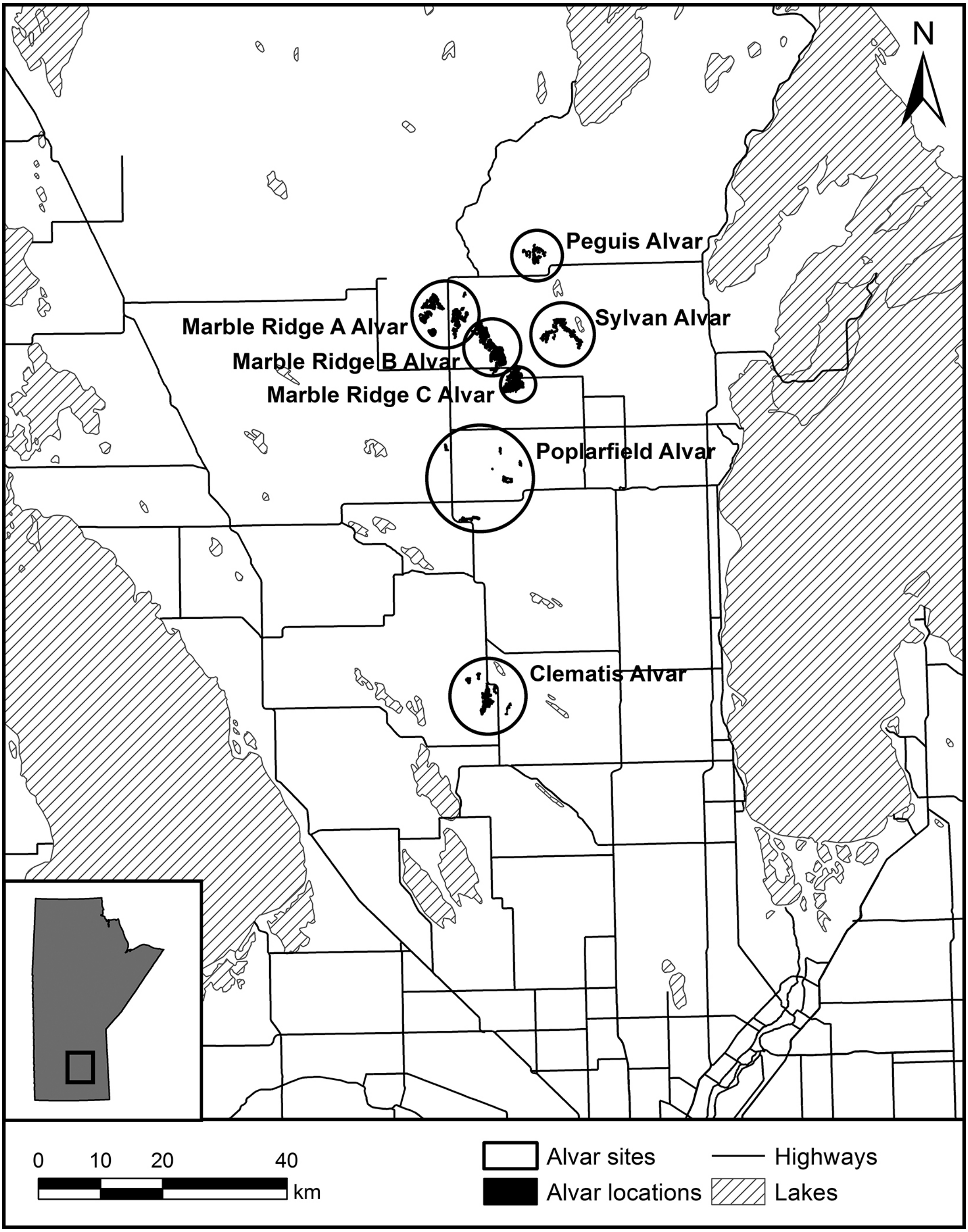

FIGURE 2. Confirmed locations of alvar in Manitoba. Individual patches of alvar have been grouped into five sites. Marble Ridge A, B, and C together constitute a single site.

In shrubland alvars (Figures 4, 5, and 6) vegetative cover is generally patchy and often restricted to cracks and seams in the bedrock with deeper soils. Soil depth is shallower than in grassland alvars, typically <5 cm, and limestone pavement is frequent. Shrubs are the dominant vascular plant cover, followed by forbs, with graminoids frequent, but not as abundant as in grassland alvars. Tree cover is greater than in grassland alvars, but still low, and trees generally appear to be stunted. Cover of bryophytes, lichens, and bare soil is much higher

Table 1. Vascular plants, bryophytes, and lichens observed in each type of alvar.

Species		Conservation status*		Alvar type			
Scientific name	Common name	Global	Subnational	Grassland	Shrubland	Savannah	Wetland
Vascular plants							
Achillea millefolium L.	Common Yarrow	G5	S5	X	X	X	
Agoseris glauca (Pursh) Rafinesque	Pale Agoseris	G5	S4S5		X	X	
Agrostis scabra Willdenow	Rough Bentgrass	G5	S5		X	X	
Agrostis stolonifera L.	Creeping Bentgrass	G5	SNA		X	X	
Allium stellatum Fraser ex Ker Gawler	Autumn Onion	G5	S5	X	X	X	
Allium textile A. Nelson & J.F. Macbride	Prairie Onion	G5	S3		X	X	
Amelanchier alnifolia (Nuttall) Nuttall ex M. Roemer	Saskatoon	G5	S5		X	X	
Ambrosia spp.	Ragweed species			X	X	X	
Andropogon gerardi Vitman	Big Bluestem	G5	S5		X	X	
Anemonastrum canadense (L.) Mosyakin	Canada Anemone	G5	S5		X	X	
Anemone cylindrica A. Gray	Long-headed Anemone	G5	S5		X	X	
Anemone multifida Poiret	Cut-leaved Anemone	G5	S5		X	X	
Antennaria spp.	Pussytoes species			X	X	X	
Anticlea elegans (Pursh) Rydberg	Mountain Death Camas	G5	S5		X	X	
Apocynum androsaemifolium L.	Spreading Dogbane	G5	S5		X	X	
Arabis hirsuta (L.) Scopoli	Hairy Rockcress	G5	S5		X	X	
Arabis sp.	Rockcress species				X	X	
Arctostaphylos uva-ursi (L.) Sprengel	Common Bearberry	G5	S5		X	X	
Artemisia campestris L.	Field Wormwood	G5	S4S5		X	X	
Artemisia ludoviciana Nuttall	Silver Wormwood	G5	S5		X	X	
Asclepias sp.	Milkweed species				X	X	
Betula occidentalis Hooker	Water Birch	G5	S3S5		X	X	
Betula papyrifera Marshall	Paper Birch	G5	S5		X	X	
Betula pumila L.	Bog Birch	G5	S5		X	X	
Bromus inermis Leysser	Smooth Brome	G5	SNA		X		
Bromus porteri (J.M. Coult) Nash	Porter's Brome	G5	S2S3	X	X	X	
Campanula gieseckeana (Vest ex Shultes)	Giesecke's Bellflower	G5	S5	X	X	X	
Carex spp.	Sedge species			X	X	X	X
Cerastium arvense L.	Field Chickweed	G5	S5		X	X	
Chenopodium spp.	Goosefoot species				X		
Cirsium drummondii Torrey & A. Gray	Drummond's Thistle	G5	S4		X	X	
Cirsium sp.	Thistle species				X	X	
Comandra umbellata (L.) Nuttall	Bastard Toadflax	G5	S5		X	X	
Corylus americana Walter	American Hazelnut	G5	S4		X	X	
Cypripedium sp.	Lady's Slipper				X	X	
Dalea purpurea Ventenat	Purple Prairie-clover	G5	S5		X	X	
Danthonia spicata (L.) P. Beauvois ex Roemer & Schultes	Poverty Oatgrass	G5	S4S5	X	X	X	
Dasiphora fruticosa (L.) Rydberg	Shrubby Cinquefoil	G5T5	S5	X	X	X	X
Deschampsia cespitosa (L.) Palisot de Beauvois	Tufted Hairgrass	G5	S4S5	X	X	X	X

TABLE 1. (*continued*)

Species		Conservation status*		Alvar type			
Scientific name	Common name	Global	Subnational	Grassland	Shrubland	Savannah	Wetland
Drymocallis arguta (Pursh) Rydberg	Tall Wood Beauty	G5	S5		X	X	
Eleocharis spp.	Spikerush species			X		X	X
Elymus trachycaulus subsp. *subsecundus* (Link) Á. Löve & D. Löve	One-sided Wildrye	G5	S5	X	X	X	
Elymus trachycaulus (Link) Gould ex Shinners	Slender Wildrye	G5T5	S5	X			
Erigeron philadelphicus L.	Philadelphia Fleabane	G5	S5		X	X	
Erigeron spp.	Fleabane species				X	X	
Festuca hallii (Vasey) Piper	Plains Rough Fescue	G4	S3		X	X	
Fragaria virginiana Miller	Wild Strawberry	G5	S5		X	X	
Gaillardia aristata Pursh	Great Blanketflower	G5	S5		X	X	
Galium boreale L.	Northern Bedstraw	G5	S5	X	X	X	
Geum triflorum Pursh	Three-flowered Avens	G5	S4S5	X	X	X	
Grindelia squarrosa (Pursh) Dunal	Curly-cup Gumweed	G5	S5	X			
Helianthus sp.	Sunflower species				X	X	
Helictochloa hookeri (Scribner) Romero Zarco	Hooker's Oatgrass	G5	S3S4		X		
Heuchera richardsonii R. Brown	Richardson's Alumroot	G5	S5		X	X	
Hieracium umbellatum L.	Umbellate Hawkweed	G5	S5		X	X	
Juncus dudleyi Wiegand	Dudley's Rush	G5	S5	X			X
Juniperus communis L.	Common Juniper	G5	S5		X	X	
Juniperus horizontalis Moench	Creeping Juniper	G5	S5	X	X	X	X
Koeleria macrantha (Ledebour) Schultes	Prairie Junegrass	G5	S5	X	X	X	
Lathyrus sp.	Vetch species				X	X	
Lepidium sp.	Peppergrass species			X	X	X	
Liatris ligulistylis (A. Nelson) K. Schumann	Meadow Blazing-star	G5?	S4		X	X	
Lilium philadelphicum L.	Wood Lily	G5	S4		X	X	
Linnaea borealis L.	Twinflower	G5	S5		X	X	
Linum lewisii Pursh	Lewis' Wild Blue Flax	G5	S4		X	X	
Lithospermum canescens (Michaux) Lehmann	Hoary Puccoon	G5	S5	X	X	X	
Lonicera dioica L.	Limber Honeysuckle	G5	S5		X	X	
Maianthemum canadense Desfontaines	Wild Lily-of-the-valley	G5	S5		X	X	
Maianthemum stellatum (L.) Link	Starflower False Solomon's Seal	G5	S5		X	X	
Medicago lupulina (L.)	Black Medick	GNR	SNA		X	X	
Melampyrum lineare Desrousseaux	American Cow-wheat	G5	S3S5		X	X	
Monarda fistulosa (L.)	Wild Bergamot	G5	S5		X	X	
Orthocarpus luteus Nutall	Yellow Owl's-clover	G5	S4S5		X	X	
Oryzopsis asperifolia Michaux	Rough-leaved Mountain Rice	G5	S5		X	X	
Pediomelum esculentum (Pursh) Rydberg	Large Indian Breadroot	G5	S3S4		X	X	
Pellaea gastonyi Windham	Gastony's Cliffbrake	G2G3	S1		X		
Pellaea glabella subsp. *occidentalis* (E.E. Nelson) Windham	Western Dwarf Cliffbrake	G5T4	S2		X		
Phleum pratense (L.)	Common Timothy	GNR	SNA	X	X	X	
Phlox hoodii Richardson	Hood's Phlox	G5	S3		X	X	

TABLE 1. (*continued*) Vascular plants, bryophytes, and lichens observed in each type of alvar.

Species		Conservation status*		Alvar type			
Scientific name	Common name	Global	Subnational	Grassland	Shrubland	Savannah	Wetland
Picea glauca (Moench) Voss	White Spruce	G5	S5		X	X	
Pinus banksiana Lambert	Jack Pine	G5	S5		X	X	
Poa annua L.	Annual Bluegrass	GNR	SNA	X	X	X	
Poa pratensis L.	Kentucky Bluegrass	G5	S5	X	X	X	
Poa sp.	Bluegrass species				X	X	
Polygala senega L.	Seneca Snakeroot	G4G5	S4		X	X	
Populus tremuloides Michaux	Trembling Aspen	G5	S5		X	X	
Potentilla anserina (L.) subsp. *anserina*	Common Silverweed	G5	S5		X	X	
Potentilla bipinnatifida Douglas ex Hooker	Bipinnate Cinquefoil	G5	SU	X			
Potentilla gracilis Douglas ex Hooker	Slender Cinquefoil	G5	S4	X			
Potentilla pensylvanica L.	Pennsylvania Cinquefoil	G5	SU	X	X		
Potentilla sp.	Cinquefoil species			X			X
Prunus pensylvanica L. f.	Pin Cherry	G5	S5		X	X	
Prunus virginiana L.	Chokecherry	G5	S5		X		
Quercus macrocarpa Michaux	Bur Oak	G5	S5		X	X	
Rhus glabra L.	Smooth Sumac	G5	S3S4		X	X	
Ribes oxyacanthoides L.	Canada Gooseberry	G5	S5		X	X	
Rosa acicularis Lindley	Prickly Rose	G5	S5	X	X	X	
Rubus idaeus L.	Red Raspberry	G5	S5		X	X	
Rudbeckia hirta L.	Black-eyed-Susan	G5	S5		X	X	
Salix spp.	Willow species				X	X	
Sanicula marilandica L.	Maryland Sanicle	G5	S5		X	X	
Selaginella densa Rydberg	Prairie Spikemoss	G5	S3		X		
Shepherdia canadensis (L.) Nuttall	Soapberry	G5	S5		X	X	
Sisyrinchium montanum Greene	Strict Blue-eyed-grass	G5	S5		X	X	
Smilax lasioneura Hooker	Hairy-nerved Carrionflower	G5	S4S5		X	X	
Solidago hispida Muhlengerg ex Willdenow	Hairy Goldenrod	G5	S5		X	X	
Solidago missouriensis Nuttall	Missouri Goldenrod	G5	S5		X	X	
Solidago nemoralis Aiton	Grey-stemmed Goldenrod	G5	S5		X	X	
Solidago ptarmicoides (Torrey & A. Gray) B. Boivin	Upland White Goldenrod	G5	S4S5		X	X	
Solidago spp.	Goldenrod species				X	X	
Symphoricarpos sp.	Snowberry species				X	X	
Symphyotrichum spp.	Aster species			X	X	X	
Symphyotrichum ericoides (L.) G.L. Nesom	White Heath Aster	G5	S4	X			
Symphyotrichum laeve (L.) Á. Löve & D. Löve	Smooth Aster	G5	S5		X	X	
Taraxacum officinale F.H. Wiggers	Common Dandelion	G5	SNA		X	X	
Thalictrum venulosum Trelease	Veiny Meadow-rue	G5	S5		X	X	
Toxicodendron radicans var. *rydbergii* (Small ex Rydberg) Erskine	Western Poison Ivy	G5	S5		X	X	
Viburnum rafinesqueanum Schultes	Downy Arrowwood	G5	S4S5		X	X	
Vicia americana Muhlenberg ex Willdenow	American Vetch	G5	S5		X	X	

TABLE 1. (*continued*)

Species		Conservation status*		Alvar type			
Scientific name	Common name	Global	Subnational	Grassland	Shrubland	Savannah	Wetland
Vicia sp.	Vetch species			X	X	X	
Viola spp.	Violet species				X		
Zizia aptera (A. Gray) Fernald	Heart-leaved Alexanders	G5	S5		X	X	
Zizia aurea (L.) W.D.J. Koch	Golden Alexanders	G5	S4S5		X	X	
MOSSES							
Abietinella abietina (Hedw.) Fleisch.	Wiry Fern Moss	G4G5	S4S5	X	X	X	
Aulacomnium palustre (Hedw.) Schwaegr.	Ribbed Bog Moss	G5	S4S5		X	X	
Barbula convoluta Hedw.	Lesser Bird's-claw Beard Moss	G5	SU	X	X	X	
Brachythecium campestre (C. Müll.) Schimp. in B.S.G	Field Ragged Moss	G4G5Q	SU		X	X	
Brachythecium salebrosum (Web. & Mohr) Schimp	Golden Ragged Moss	G5	S4S5		X	X	
Brachythecium sp.					X	X	
Bryum sp.				X	X	X	
Campylium polygamum (Schimp.in B.S.G) C. Jens.	Campylium Moss	G5	S4S5	X	X	X	
Ceratodon purpureus (Hedw.) Brid.	Red Roof Moss	G5	S4S5		X	X	
Dicranum polysetum Sw.	Wavy-leaf Broom Moss	G5	S4S5		X	X	
Didymodon rigidulus Hedw.	Rigid Beard Moss	G5	SU	X	X	X	
Encalypta procera Bruch	Slender Candlesnuffer Moss	G4G5	SU		X	X	
Eurhynchium pulchellum (Hedw.) Jenn.	Elegant Beaked Moss	G5	S4S5		X	X	
Grimmia teretinervis Limpr.	Round-nerved Grimmia	G3G5	SNR		X	X	
Hedwigia ciliata (Hedw.) P. Beauv.	Ciliate Hedwig's Moss	G5	SU		X	X	
Hylocomium splendens (Hedw.) Schimp. in B.S.G	Stairstep Moss	G5	S4S5		X	X	
Pleurozium schreberi (Brid.) Mitt.	Red-stemmed Feather Moss	G5	S4S5		X	X	
Ptychostomum pseudotriquetrum (Hedw.) J.R. Spence & H.P. Ramsay	Tall Clustered Thread Moss	G5	S4S5	X			
Sanionia uncinata (Hedw.) Loeske	Sickle Moss	G5	S4S5		X	X	
Syntrichia norvegica Web.	Norway Screw Moss	G5	SU		X	X	
Tortella fragilis (Hook. & Wils. in Drumm.) Limpr.	Fragile Twisted Moss	G5	S4S5	X	X	X	
Tortella tortuosa (Hedw.) Limpr.	Frizzled Crisp Moss	G5	SU		X	X	
Tortula ruralis (Hedw.) Gaertn. *et al.*	Hairy Screw Moss	G5	S4S5	X	X	X	
LICHENS							
Biatora vernalis (L.) Fr.	Spring Dot Lichen	G5	S3S5		X		
Mycobilimbia sabuletorum (Schreb.) Hafellner	Six-celled Moss Dot Lichen	G5	S2S4		X		
Caloplaca holocarpa (Hoffm. ex Ach.) A. E. Wade	Firedot Lichen	G5	S3S5		X	X	
Caloplaca jungermanniae (Vahl) Th. Fr.	Jungermann's Firedot Lichen	G4G5	S2S4		X		
Cladina arbuscula (Wallr.) Hale & Culb.	Reindeer Lichen	G5	S5		X	X	
Cladonia botrytes (K. G. Hagen) Willd.	Wooden Soldiers Lichen	G5	S4			X	
Cladonia cariosa (Ach.)	Split-peg Lichen	G5	S5		X		
Cladonia cervicornis ssp. verticillata (Hoffm.) Ahti	Ladder Lichen	G5T5	S4		X		
Cladonia chlorophaea (Flörke ex Sommerf.)	Mealy Pixie-cup Lichen	G5	S5		X		
Cladonia cristatella Tuck.	British Soldiers	G5	S5			X	

TABLE 1. (*continued*) Vascular plants, bryophytes, and lichens observed in each type of alvar.

Species		Conservation status*		Alvar type			
Scientific name	Common name	Global	Subnational	Grassland	Shrubland	Savannah	Wetland
Cladonia macrophyllodes Nyl.	Large-leaved Pixie Lichen	G4G5	SU		X		
Cladonia multiformis G. Merr.	Sieve Lichen	G5	S5		X		
Cladonia pocillum (Ach.) Grognot	Rosette Pixie-cup Lichen	G5	S4		X	X	
Cladonia pyxidata (L.) Hoffm.	Pebbled Pixie-cup	G5	S5		X		
Cladonia ramulosa (With.) J. R. Laundon	Branched Pixie-cup Lichen	G5?	SU			X	
Cladonia symphycarpa (Flörke) Fr.	Split-peg Lichen	G5	S4		X	X	
Peltigera praetextata (Flörke ex Sommerf.) Zopf	Scaly Pelt Lichen	G5	SU		X		
Peltigera rufescens (Weiss) Humb.	Felt Lichen	G5	S5		X	X	
Physcia adscendens (Fr.) H. Olivier	Hooded Rosette Lichen	G5	S5		X	X	
Physcia aipolia (Ehrh. ex Humb.) Fürnr.	Hoary Rosette Lichen	G5	SU		X	X	
Physcia phaea (Tuck.) J. W. Thomson	Black-eyed Rosette Lichen	G4G5	SU	X			
Sarcogyne regularis Körber	Frosted Grain-spored Lichen	G5	S3S5		X		
Stereocaulon paschale (L.) Hoffm.	Easter Foam Lichen	G5	SU		X		
Verrucaria muralis Ach.	Wart Lichen	G5	S2S4		X		
Xanthoparmelia cumberlandia (Gyelnik) Hale	Cumberland Rock-shield	G5	SU		X		
Xanthoria polycarpa (Hoffm.) Th. Fr. ex Rieber	Pincushion Sunburst Lichen	G5	S4		X	X	
LIVERWORTS							
Cephaloziella rubella (Nees) Warnst	Red Threadwort	G5	SU		X	X	

*Global (NatureServe 2016) and subnational (Manitoba Conservation Data Centre unpubl. data) conservation status ranks.

FIGURE 3. Grazed grassland alvar at the Sylvan Alvar site. Photo: Nature Conservancy of Canada.

FIGURE 4. Shrubland alvar at the Clematis Alvar site. Photo: Nature Conservancy of Canada.

FIGURE 5. At the Clematis Alvar site, trees are often present along the periphery where the alvar transitions into woodland. Photo: Nature Conservancy of Canada.

FIGURE 6. Shrubland alvar at the Marble Ridge Alvar site. Some of the scattered boulders support Gastony's Cliffbrake (*Pellaea gastonyi*) or Western Dwarf Cliffbrake (*Pellaea glabella* ssp. *occidentalis*) or both. Photo: Nature Conservancy of Canada.

than in grassland alvars, although the abundance of each varies among sites. Sites vary from flat to having table-top limestone outcrops and scattered limestone boulders. Drainage is restricted at these sites, which are periodically flooded. In the absence of rain, drought-like conditions were observed.

Savannah alvars (Figures 7 and 8) are similar to shrubland alvars in their patchy distribution of vegetation. Soil depth is usually <5 cm, but frequently deeper in cracks and seams. Limestone pavement is frequent. Shrubs are dominant, followed by forbs, with graminoids less abundant. Unlike shrubland alvars, distribution of trees is regular, although still amounting to <60% cover, and tall shrubs can occur frequently. Bryophyte and lichen cover is variable and generally less dominant than in shrubland alvars. Like shrubland alvars, savannah alvars vary from being flat to having scattered boulders or table-top outcrops, but are more frequently associated with the latter than shrubland alvars. These sites flood periodically and exhibit drought-like conditions; however, extremes in moisture variability at sites with greater tree abundance are not as pronounced.

Like grassland alvars, wetland alvars have nearly continuous vegetative cover, with soils about 5 cm deep and occasional patches of exposed limestone pavement (Figure 9). They are dominated by wetland graminoids and mosses, with few forbs or shrubs and no trees. These are low areas that grade into other alvar types. They are often partly bordered by willow-dominated swamps and marsh. Despite similar soil depths and cover as grassland alvars, these sites remain saturated enough to support wetland vegetation, but are not permanently flooded. It is unknown whether the difference is a result of increased water catchment from the surrounding topography or a difference in the degree of drainage restriction by the underlying bedrock.

Bedrock geology

Survey sites coincided with limestone bedrock from the Jurassic, Permian, Devonian, Silurian, and Ordovician geologic periods. Alvar was located only on Silurian and Ordovician bedrock, which consist primarily of dolomite (Manitoba Mineral Resources 2012a).

The Clematis Alvar and two units of the Poplarfield Alvar occur on Silurian bedrock, which consists of micritic, fossiliferous, stromatolitic, and biostromal dolomites, whereas the other alvars occur on Ordovician bedrock comprising various dolomites including argillaceous, nodular, and laminated dolomite (Manitoba Mineral Resources 2012a).

Alvars occur on four Ordovician formations. The Marble Ridge Alvar site and the rest of the Poplarfield Alvar sites are primarily located within the western

FIGURE 7. Savannah alvar with White Spruce (*Picea glauca*) at the Poplarfield Alvar site. Photo: Nature Conservancy of Canada.

FIGURE 8. Savannah alvar with Jack Pine (*Pinus banksiana*) at the Marble Ridge Alvar site. Photo: Nature Conservancy of Canada.

FIGURE 9. Wetland alvar at the Marble Ridge Alvar site. Photo: Nature Conservancy of Canada.

Stony Mountain Formation and the East Arm Formation, whereas the Peguis and Sylvan Alvars fall into the eastern Stony Mountain Formation and the Red River Formation (Manitoba Mineral Resources 2012a).

Significant species

Twenty-four globally, nationally, or provincially rare and uncommon species (NatureServe 2016; Manitoba Conservation Data Centre unpubl. data) were documented at survey sites during this study or previously by Caners (2011). Globally uncommon and provincially endangered Gastony's Cliffbrake (*Pellaea gastonyi* Windham; Friesen and Murray 2015) and globally uncommon Grimmia Dry Rock Moss (*Grimmia teretinervis* Limpricht; Caners 2011) were observed growing on limestone cliffs and boulders at the Marble Ridge Alvar sites. Vascular plant species assessed as provincially uncommon or rare (Manitoba Conservation Data Centre unpubl. data) observed during this study include: Dwarf Western Cliffbrake *(Pellaea glabella* ssp. *occidentalis* (E.E. Nelson) Windham), Rough Fescue (*Festuca hallii* (Vasey) Piper), Porter's Chess (*Bromus porteri* (J.M. Coulter) Nash), Wild White Onion (*Allium textile* A. Nelson & J.F. Macbride), Spring Birch (*Betula occidentalis* Hooker), Spike-oat (*Avenula hookeri* (Scribner) Holub), American Cow-wheat (*Melampyrum lineare* Desrousseaux), Large Indian Breadroot (*Pediomelum esculentum* (Pursh) Rydberg), Smooth Sumac (*Rhus glabra* L.), and Dense Spikemoss (*Selaginella densa* Rydberg; Table 1). Six species of lichens observed during this study and six species of bryophytes documented by Caners (2011) are also assessed as nationally or provincially rare or uncommon (NatureServe 2016; Manitoba Conservation Data Centre unpubl. data).

Six non-native plant species were observed in alvars. Timothy (*Phleum pratense* L.) was observed often, but never as a dominant species. Kentucky Bluegrass (*Poa pratensis* L.) was observed in some grass-dominated alvars. Annual Bluegrass (*Poa annua* L.) was observed in some alvars, often occurring on sparsely vegetated patches of shallow, bare soil. Garden Bird's-foot Trefoil (*Lotus corniculatus* L.) was found on the periphery of two alvars and, at a third site, there were a few scattered plants on the alvar itself. Awnless Brome (*Bromus inermis* Leysser) and Creeping Bentgrass (*Agrostis stolonifera* L.) were each observed once in a grazed alvar.

Overall, it appears that non-native species in Manitoba alvars are infrequent, and invasive species that are of high priority for detection and control in Manitoba (Invasive Species Council of Manitoba 2018) are not currently present in these ecosystems. Non-native or invasive plant species can result in reduced biodiversity and function in natural ecosystems and are becoming increasingly widespread in open habitats in the prairie provinces (Canadian Food Inspection Agency 2008; Sinkins and Otfinowski 2012; DeKeyser *et al.* 2013). The relatively limited presence of non-native or invasive species in Manitoba alvars represents a rare opportunity to prevent further establishment and maintain the exceptional biodiversity of these habitats.

Management and conservation context

Alvars make up 0.3% (3934 ha) of the south Interlake. Each alvar type supports its own complement of plants and contributes uniquely to the biological diversity of Manitoba. The significance of alvar habitat and the threats it faces across Canada have been extensively documented (Catling and Brownell 1995, 1999b; Reschke *et al.* 1999; Catling 2014; Catling *et al.* 2014; Brunton and Catling 2017). Protection and conservation efforts in Manitoba should initially focus on preserving representatives of each type. In addition to supporting vascular plant species assemblages distinct from other ecosystems in Manitoba, different types of alvar support a range of other species groups. For example, we observed grassland-obligate birds, a group undergoing steep population declines in North America (North American Bird Conservation Initiative 2016), on grassland alvars; Eastern Whip-poor-will (*Antrostomus vociferus*) and Common Nighthawk (*Chordeiles minor*), both threatened species (SARA Registry 2018a,b), have been documented in shrubland and savannah alvars with sparse vegetation (Manitoba Conservation Data Centre unpubl. data). Alvars associated with inland cliffs, outcrops, and boulders, such as along Marble Ridge, provide a wide range of microhabitats not found in other alvar types, and support a number of bryophytes that are expected to remain uncommon in the region (Caners 2011).

Approximately one third (1261 ha) of alvar in Manitoba occurs on privately owned land, with the remainder on public land including wildlife management areas, community pastures, and undesignated provincial Crown land.

No alvar sites identified in this study are located within the boundaries of protected areas (IUCN Protected Areas Classification level IV or higher; Manitoba Conservation and Water Stewardship 2012b) or are protected from all types of development. A 2560-ha ecosystem protection zone that encompasses most of the Marble Ridge Alvar site has been proposed.

Approximately 12% of the Manitoba alvar habitat identified in this study falls under mining and/or quarry leases (Manitoba Mineral Resources 2012b) and, thus, may be exposed to habitat destruction from mining activities. At the time of our survey, near-surface limestone had been commercially extracted immediately adjacent to or within alvar communities at six locations.

Approximately 76% (2985 ha) of alvar habitat identified in this study was being grazed at the time of the survey or exhibited signs of having been grazed recently. Another 11% (432 ha) did not appear to be grazed by domestic livestock. Most observed grazing animals were cattle, but horses and bison were also observed. Land use at the other locations (13%) could not be determined. Pre-European settlement grazing histories for the Interlake area are unclear (Henderson and Koper 2014), but grazing by large ungulates has likely always contributed to the disturbance regime of Manitoba alvars and may play an important role in maintaining their openness, as it does in alvars elsewhere (Reschke *et al.* 1999). However, current grazing management using livestock is unlikely to mirror historical patterns (Henderson and Koper 2014), and grazing at incompatible frequencies, intensities, or durations may result in alterations to species composition and facilitate the spread of non-native species (Reschke *et al.* 1999).

No evidence of recent natural fire, an important ecological requirement of many alvar habitats (Catling and Brownell 1998; Catling *et al.* 2002; Jones and Reschke 2005; Catling 2009b), was observed in or near any of the alvars. Trembling Aspen (*Populus tremuloides* Michaux) encroachment was observed at some locations in the Clematis Alvar and Poplarfield Alvar sites. Long-term fire suppression is probably negatively impacting the ecological integrity and biodiversity of alvar habitat here, as it is in other open habitats in southern Manitoba (e.g., Koper *et al.* 2010) and throughout North America.

The current mix of public and private land ownership, history of fire suppression, and the economic potential of alvars for grazing and mineral resources highlight the need for the involvement and cooperation of a range of stakeholders, including industry and private landowners, in alvar conservation.

Further research

This study presents only a first approximation of the various types of alvar present in Manitoba, and there is a need for classification of alvar habitat in the province using a quantitative data-based scheme. This would help to refine the conservation status of alvar types/subtypes and to inform site-condition metrics, compatible land-management activities, and conservation opportunities. Faunal surveys to further assess the biodiversity of these sites are also needed. The selection of appropriate conservation management options in Manitoba requires full investigation of the relation between the ecological integrity of alvar habitat and ecological processes, such as grazing and fire suppression.

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New avian breeding records for Kugluktuk, Nunavut

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Abstract

New breeding records for 10 species of tundra and boreal nesting birds were documented near the community of Kugluktuk (Nunavut, Canada) over the course of the 2015 and 2016 breeding seasons and incidentally in 2017 and 2018. These species include American Wigeon (*Mareca americana*), Mallard (*Anas platyrhynchos*), Northern Shoveler (*Anas clypeata*), Green-winged Teal (*Anas carolinensis*), Greater Scaup (*Aythya marila*), Say's Phoebe (*Sayornis saya*), Canada Jay (*Perisoreus canadensis*), Grey-cheeked Thrush (*Catharus minimus*), Yellow-rumped Warbler (*Setophaga coronata*), and Dark-eyed Junco (*Junco hyemalis*). Previously unpublished breeding evidence for Bald Eagle (*Haliaeetus leucocephalus*) is also discussed along with suspected breeding of Barn Swallow (*Hirundo rustica*), Bohemian Waxwing (*Bombycilla garrulus*), White-throated Sparrow (*Zonotrichia albicollis*), and Pine Grosbeak (*Pinicola enucleator*). These records represent the first described breeding occurrences for these species in the Kitikmeot region, or new records for the mainland of Nunavut. A lack of historical ornithological survey effort in this area has likely led to the diversity of these previously unrecorded breeding observations. These results highlight the need to increase geographic coverage of bird surveys in northern Canada to more accurately delineate the northern limit of breeding ranges and suggest that further formal survey effort will undoubtedly lead to additional new breeding records.

Key words: Breeding records; range extensions; Arctic; Nunavut; Kugluktuk

Introduction

Located in the westernmost portion of Nunavut, Kugluktuk boasts some of the greatest diversity of terrestrial flora (Saarela *et al.* 2017) and fauna in the territory (Lamont and Knaggs 2016; eBird 2017). The region is also well known for harbouring robust populations of diurnal birds of prey, observed during surveys in the 1980s and 1990s before the establishment of Nunavut (Bromley and McLean 1986; Shank *et al.* 1990) and confirmed through more recent raptor surveys (Lamont *et al.* 2016, 2018).

Until recently, little ornithological survey activity has occurred near the hamlet of Kugluktuk. Previous surveys in the mid-2000s were made from rotary and fixed-wing aircraft and targetted mainly breeding waterfowl (Conant *et al.* 2007; Groves and Mallek 2011) or nesting raptors (Bromley 1982; Bromley and McClean 1986; Shank 1996; Lamont *et al.* 2016). Such methods lack the precision needed to detect young or nests, particularly of Passeriformes. In spring 2017, the first set of the Arctic Program for Regional and International Shorebird Monitoring (PRISM) surveys was undertaken around Kugluktuk by the Canadian Wildlife Service (J. Rausch pers. comm. 6 June 2017).

This overall lack of survey effort, compared with other parts of the territory, which have seen years or decades of ornithological research and amateur birding (e.g., Bylot Island, Cambridge Bay, Coats Island), has resulted in a potential gap in our understanding of the true breeding range of some avian species in the western Kitikmeot. The proximity of the treeline to Kugluktuk, in addition to the northward flow and funnelling valleys of the Coppermine, Richardson, and Rae Rivers, all contribute to the presence of species in the region that are normally only found at much lower latitudes elsewhere in the territory. Summarized herein are observations of detected nests and recently fledged young for 10 species of birds, previously lacking breeding evidence for the territory or for the Kitikmeot region. I follow the recent examples of Hussell *et al.* (2012) and Lecomte and Giroux (2015), who highlight the importance of documenting and reporting new breeding records in Nunavut to help expand our knowledge of avian distributions in the Canadian Arctic and to potentially aid in detecting changes in bird communities at given locations over time.

Methods

Kugluktuk is located in the western Kitikmeot region of Nunavut, at the mouth of the Coppermine River (67.81°N, 115.09°W; Figure 1). This area is within the Southern Arctic Terrestrial Ecozone (Wilken 1986): mean annual temperature is −11°C, mean summer temperature 5°C, and mean winter temperature −26°C, average annual precipitation 200 mm (northern part of the region) to 300 mm (southern portions). A nearly continuous cover of shrub tundra vegetation exists, consisting of Alaska Willow (*Salix alaxensis* (Andersson) Coville var. *alaxensis*), Arctic Willow (*Salix arctica* Pallas), Dwarf Birch (*Betula glandulosa* Michaux), Alpine Bearberry (*Arctostaphylos alpina* (L.) Niedenzu), Dwarf Labrador Tea (*Rhododendron tomentosum* subsp. *decumbens* (Aiton) Elven & D. F. Murray), and *Dryas* spp. and sedge (*Carex* spp.) tussocks (Wilken 1986). The proximity to the treeline and the more temperate microclimates associated with the Coppermine, Rae, and Richardson River valleys, provide shelter from harsh Arctic winds for a variety of plant species.

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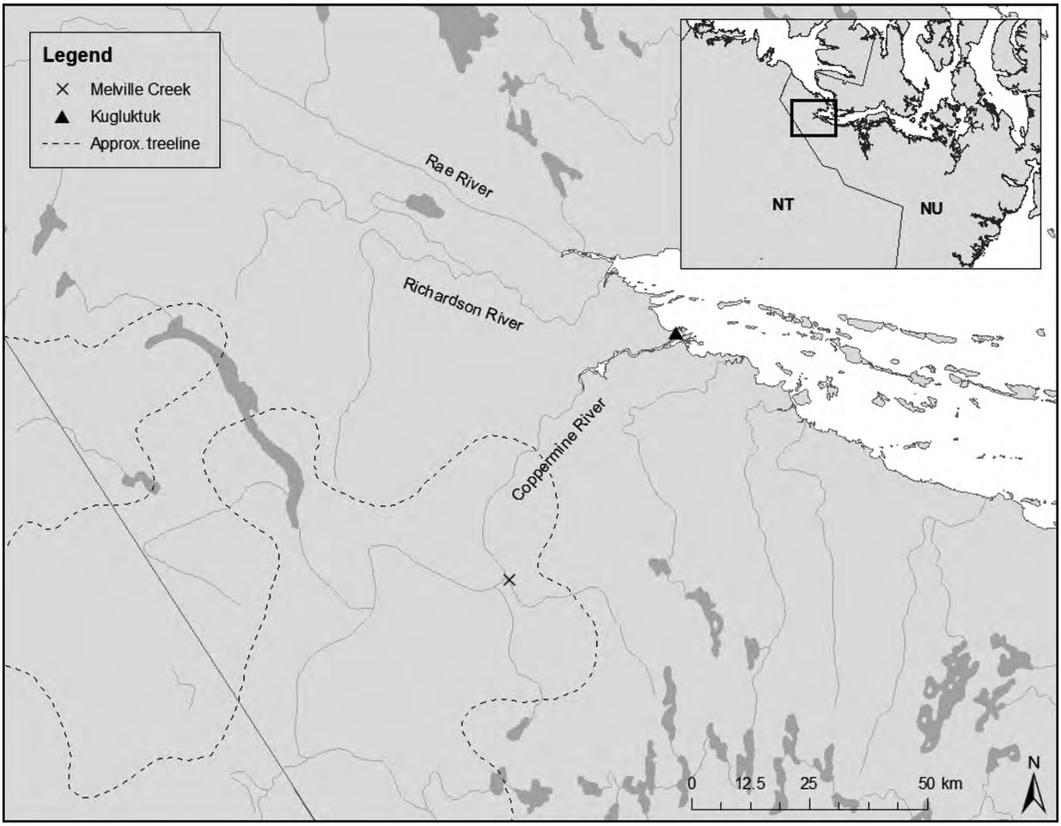

FIGURE 1. Location of the study area, Kugluktuk, Nunavut depicting the Rae, Richardson and Coppermine Rivers and the location of Melville Creek, south of Kugluktuk.

I conducted localized, visual, ground surveys within a 20-km radius (unless otherwise noted) of Kugluktuk. Incidental observations and surveys were undertaken throughout the year, from 1 January 2015 through 31 August 2016 while I was living in the hamlet, with an additional week of observations in July 2017 and one week in June and July 2018, respectively. All ground observations were made on the west side of the Coppermine River. Ground surveys were undertaken systematically following Arctic PRISM protocols (Bart and Johnson 2012), through targetted habitat surveys and opportunistic encounters. Nests and/or recently fledged young were documented to confirm breeding activity.

Results and Discussion

AMERICAN WIGEON (*Mareca americana*)

During the 2015–2016 field seasons, this species was observed feeding in local wetlands, ephemeral pools, and ponds around Kugluktuk, often with other species of waterfowl such as Northern Pintail (*Anas acuta*) and Mallard (*Anas platyrhynchos*). On 13 July 2016, a female was flushed from a small pond, accompanied by nine ducklings of age subclass Ia (Figure S1).

American Wigeon is known to favour taiga environments and is often found in the transition zone between boreal and tundra ecozones (Silver *et al.* 2012; Mini *et al.* 2014) and on Akimiski Island (K. Abraham pers. comm. 21 August 2016); however, despite these habitat preferences, relatively few records exist for Nunavut. The first documented breeding evidence was recorded by Harper (1953) near Windy River (south Kivalliq); one other observation of recently fledged young occurred in Bathurst Inlet in 1996 (eBird 2017). The breeding record described here is believed to be only the second and northernmost breeding evidence for the territory.

MALLARD (*Anas platyrhynchos*)

In 2015, several pairs of Mallards were observed in the vicinity of Kugluktuk, occupying small ponds and foraging in ephemeral pools. Pursuit flights were often observed during the spring months. On 13 July 2016, a female was flushed from the edge of a small pond with two young, approximately age subclass Ib (Figure S2).

Although Mallard has a wide distribution and is considered a habitat generalist (Drilling *et al.* 2018), only sporadic observations of this species exist north of the treeline (eBird 2017). The only previous confirmed breeding records in Nunavut are from James Bay on Stag Rock, where a nest with ten eggs was found on 26 June 1995 (Tymstra 1997) and near Windy River, where young and nests have been observed (Harper 1953). The record described here is believed to be the westernmost and northernmost breeding evidence for the territory and the first for the Kitikmeot region.

NORTHERN SHOVELER (*Anas clypeata*)

Sightings of this species occurred regularly throughout the 2015–2016 seasons. On 18 May 2015, six males and five females were observed, followed by two pairs on 31 May, and eight males and only one female on 21 June. On 24 June, a female was flushed from a nest. The clutch consisted of nine eggs and was located in a small, wet sedge meadow approximately 20 m from a small pond (Figure S3). Several pairs were again seen in 2016, although no nesting was confirmed.

Few observations of this species exist in northern Canada (J. Richards pers. comm. 23 August 2016; eBird 2017). It is present throughout the coast of James Bay in Ontario and on the west side of Hudson's Bay (Ross and North 1983; eBird 2017); however, there are no nesting records for Nunavut except one on Akimiski Island from 21 May 2001 (K. Abraham pers. comm. 19 March 2016). Several pairs have recently been observed in Cambridge Bay (S. Menu pers. comm. 10 June 2016; eBird 2017). The breeding record described here is believed to be the first for mainland Nunavut and the northernmost breeding evidence for the territory.

GREEN-WINGED TEAL (*Anas carolinensis*)

Regularly seen in both 2015 and 2016, with more males than females observed in both years, this species made extensive use of small ponds and ephemeral pools for breeding, feeding, moulting, and rearing young. In 2015, pursuit flights and courtship were observed with breeding suspected. On 13 July 2016, a young duckling of age subclass Ia was seen feeding on the surface of a pond and the female later flushed (Figure S4). Two flightless males in mid-moult were also flushed from the same area. On 20 July 2016, a second brood of eight young of age subclass Ib was encountered in the same location.

Although this species is usually associated with boreal ecosystems (Johnson 1995), a surprising number of records exist above the treeline in Nunavut, but most lack breeding evidence (eBird 2017). A female with 10 young was observed on Carey Island, James Bay, on 21 June 1995 (Tymstra 1997), and Harper (1953) describes records of young birds near Simon's Lake in the southern Kivalliq region. Beyond these two records, little evidence has been formally described in the literature for Nunavut. The breeding record described here is believed to be the westernmost and northernmost breeding evidence for the territory and the first for the Kitikmeot region.

GREATER SCAUP (*Aythya marila*)

Numerous pairs of this species were observed in both 2015 and 2016. Multiple pairs were observed feeding in shallow ponds or pools, some ephemeral. In 2015, courtship behaviours were observed, but no nests or fledged young were found. On 13 July 2016, a female was flushed from a nest (Figure S5) in a sedge meadow, in close proximity to where courtship was detected the previous year. The clutch consisted of eight eggs and appeared to be in a late stage of incubation based on the size of the air cell. On 26 July 2016, 12 males and three females with 28 ducklings were observed on a large pond 10 km west of Kugluktuk. Broods were all approximately the same age and appeared to be of subclass Ib.

Mainly restricted to coastal tundra from Alaska east to Hudson's Bay and the Nunavik region (Kessel *et al.* 2002), this species has been found in low densities from Kugluktuk to Cambridge Bay, through the Queen Maud Gulf and in inland areas of the southern Kivalliq region (Conant *et al.* 2007; Groves and Mallek. 2011; eBird 2017). Harper (1953) describes the species as breeding in southern Kivalliq, but suggests that they do not extend appreciably into the barren grounds. The record described here is believed to be the westernmost and northernmost breeding evidence for the territory and the first for the Kitikmeot region.

SAY'S PHOEBE (*Sayornis saya*)

On 24 May 2016, one male was observed within the town limits of Kugluktuk. The bird responded aggressively to recorded calls of conspecifics. On 28 May 2016, two birds were seen near a large cliff face 100 m south of the initial observation. On 19 June, only one bird was observed, feeding and returning to a large cracked rock slab that created a small crevice about 20 m up the cliff wall. The bird would continually feed and return to this location, occasionally entering the structure and returning into view several minutes later. On 21 July 2016, both adults were observed carrying food to the same location and presumably feeding a chick. On 26 July 2016, a second breeding pair was observed carrying food, and a young bird was heard begging along a cliff face, approximately 1 km south of the previous site. A nest was soon detected under a rock overhang about 2 m above the ground (Figure S6) with two infertile eggs still present. A single fledged young was observed, nearly adult size, and capable of extended flight. This same nest location was visited exactly one year later and found to have been active that season with one infertile egg still present. The same site was visited again in June and July 2018 and was active.

The timing of arrival of this species in Kugluktuk is consistent with what is known for male and female arrival on territories (Dawson 1923; Johnsgard 1979) despite its northern latitude. Both observed nesting sites were typical of what has been described for the species (Bent 1942; Schukman *et al.* 1976). It is worth noting that the abandoned nest discovered with two infertile eggs in 2016 was removed for photographic and archival purposes and was rebuilt in exactly the same fashion and location, with nearly identical nesting materials and re-occupied, presumably, by this same pair in the 2017 season. This same process of nest removal and archiving was repeated in 2017 after the nest was abandoned, and re-made and reused in 2018 as it was the previous year. Of interest were two observations of territorial birds responding to playback during a raptor survey in July 2017: one record 70 km west of Kugluktuk and another 30 km east of Kugluktuk. It is likely that additional surveys in the Kitikmeot, particularly on rock bluffs with a southern aspect, would result in a number of additional breeding records.

Only one previous breeding record for Nunavut exists, this being a photographed nest site on a shed on Nauyak Lake on Kent Peninsula on 28 June 2008 (J. Richards pers. comm. 11 June 2016; eBird 2017). The records described here are believed to be the westernmost confirmed breeding evidence for the territory.

CANADA JAY (*Perisoreus canadensis*)

A pair and two juveniles were seen and photographed on 24 July 2018 (Figure S7) near the confluence of Melville Creek and the Coppermine River ~60 km south of the Kugluktuk. Multiple birds were heard calling. The species has apparently been established along the treeline for many years (A. Niptanatiak pers. comm. 25 July 2018) and has likely gone unnoticed by ornithologists due to a lack of survey effort. Habitat was dominated by Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh), including relatively large specimens, upwards of 50 cm in diameter and 10 m tall, with an understorey of waist high Dwarf Birch, *Salix* sp., Shrubby Cinquefoil (*Dasiphora fruticosa* (L.) Rydberg), and a carpet of moss. The ecology was very similar to boreal forest found further south, with the sheltered river valley providing refugia for this habitat to proliferate. The records described here are believed to be the northernmost confirmed breeding evidence for the territory (Richards and Gaston 2018).

GRAY-CHEEKED THRUSH (*Catharus minimus*)

I observed a recently fledged juvenile on 24 July 2018 (Figure S8) near the confluence of Melville Creek and the Coppermine River ~60 km south of Kugluktuk. The chick still had downy feathers on his crown and nape. Multiple birds were heard calling prior to the sighting. Habitat conditions were similar to those described for Canada Jay. The records described here are believed to be the northernmost breeding evidence for the territory (Richards and Gaston 2018).

YELLOW-RUMPED WARBLER (*Setophaga coronata*)

I observed a pair of birds in a willow thicket within the hamlet limits on 8 June and again on 20 June 2015, followed by observations of a singing male over the course of June and July 2015. In 2016, only a single male was observed, but it was seen singing from the second week of June until the end of the month in the same location as the previous year. On 23 July 2016, a male was seen carrying food in Kugluk/Bloody Falls Territorial Park, about 13 km south of Kugluktuk. The male was observed feeding a recently fledged young (Figure S9). On 19 July 2017, a male was seen feeding a fledged young capable of sustained flight within the hamlet limits of Kugluktuk. On 24 July 2017, another male was seen feeding a recently fledged young 30 km northeast of Kugluktuk.

Kugluktuk is the only community in Nunavut with consistent sightings of this species since at least 2003 (eBird 2017); all are believed to be of the Myrtle group, *Setophaga coronata hooveri*. Previous recordings are known from the James Bay area, including Akimiski and smaller islands (Tymstra 1996, 1997), as well as in the Nueltin Lake area (Harper 1953; Mowat and Lawrie 1955). The first eBird records for Kugluktuk are of two birds (sexes not mentioned) on 11 June 2003, a single bird on 28 June 2013, and three birds (sexes not mentioned) in the adjacent Richardson River Valley on 13 August 2010. The records described here are believed to be the first confirmed breeding evidence for Nunavut.

DARK-EYED JUNCO (*Junco hyemalis*)

I observed an adult carrying food and subsequently feeding a recently fledged juvenile on 24 July 2018 at the confluence of Melville Creek and the Coppermine River (Figure S10). Habitat conditions were similar as those described for Canada Jay. The record described here is believed to be the northernmost confirmed breeding evidence for the territory.

BARN SWALLOW (*Hirundo rustica*)

A pair was observed in Kugluktuk for two consecutive breeding seasons, on 30 May 2015 and 13 June 2016. On 19 July 2015, a pair was observed near an unoccupied building within the hamlet limits. The pair began alarm calling as I approached and was later seen carrying insects. On 19 June 2016, a pair was seen collecting mud within the hamlet limits. No observations were made of this species in 2017–2018; however, survey effort was minimal compared with 2015 and 2016.

Many Barn Swallows have been seen in the Canadian Arctic (eBird 2017), but only one confirmed nesting exists for Nunavut: on a tower on Akimiski Island in July 1999 (K. Abraham unpubl. data). Late nest construction was observed in Arviat on 6 August 2008 (Eckert 2009) and a pair was seen in Rankin Inlet in 2016 (eBird 2017), but otherwise no confirmed nesting has been reported on the mainland portion of the territory. Further study in the Kugluktuk area may lead to eventual nesting detection. The records described here are believed to be the northernmost evidence for suspected breeding in the territory.

BOHEMIAN WAXWING (*Bombycilla garrulus*)

I observed what is believed to have been a pair within the hamlet limits of Kugluktuk on 23 June 2018 (Figure S11). They were feeding on Black Crowberry (*Empetrum nigrum* L.) from the previous season. Playback calls were made which generated minor response. It is likely that these birds overshot their migration past the treeline ~40 km south which would have provided suitable breeding habitat. An earlier observation from Kugluktuk was made between 19 July to 6 August 1989, however this was a single bird (Richards and Gaston 2018). This is believed to be the northernmost record of a pair in suitable habitat for the territory and breeding in this region is highly suspected.

WHITE-THROATED SPARROW (*Zonotrichia albicollis*)

I documented multiple singing males of this species on 24 July 2018 near the confluence of Melville Creek and the Coppermine River. Habitat conditions were similar to those described for Canada Jay. Calling males were in suitable habitat and breeding was highly likely. A male specimen from Kugluktuk (Richards and Gaston 2018) was collected by F.W. Schueler in 1975. This area likely represents the northernmost extent of potential breeding for the territory.

PINE GROSBEAK (*Pinicola enucleator*)

I documented a singing male on 24 July 2018 (Figure S12) near the confluence of Melville Creek and the Coppermine River. Habitat conditions were similar to those described for Canada Jay. The bird was in suitable habitat and appeared to be moulting. The record described here is believed to be the northernmost evidence for suspected breeding in the territory.

BALD EAGLE (*Haliaeetus leucocephalus*)

Two adult Bald Eagles, believed to be a pair based on courtship pursuit flights, were documented near the mouth of the Coppermine River and in Kugluk/Bloody Falls Territorial Park for the 2015–2016 breeding seasons. Territorial chasing between these two birds and a resident breeding pair of Golden Eagles (*Aquila chrysaetos*) was observed on multiple occasions, although no nests of Bald Eagles were located. Additional observations of both adult and sub-adult Bald Eagles were made in late July 2017 in both Kugluk/Bloody Falls Territorial Park and near the mouth of the Rae River.

A review of unpublished data from the jointly managed Government of Northwest Territories and Nunavut/NWT Raptor Database (2017) revealed a single record of a Bald Eagle sitting on a nest approximately 3 km southeast of Bloody Falls on 8 May 1993. In 2017, the same site was found to be an occupied Golden Eagle territory. Local ecological knowledge suggests that this species has been regularly occupying this region for nearly a decade and an experienced local resident has suggested that a pair's nest was removed during deactivation of a Distant Early Warning radar tower at Cape Young (Pin-2, 68.935°N, 116.936°W) in the mid 2000s, 150 km northwest of Kugluktuk (A. Niptanatiak pers. comm. 20 July 2018). Over the last several years, irruptive behaviours have been documented for this species in the Queen Maud Gulf (K. Drake pers. comm. 15 August 2016), and further surveys in this area will likely result in additional breeding records. The previously unpublished record from 1993 represents what is believed to be the first breeding record for the territory.

Conclusion

Whether breeding of the described species in the western Kitikmeot has occurred relatively recently as a result of climatic shifts or has simply been undetected because of a paucity of surveys remains unknown. Avian species ranges are known to be highly dynamic and subject to influence from both climatic and local environmental factors (Parmesan 2006; Virkkala *et al.* 2008, 2010, 2014). The proximity of Kugluktuk and the western Kitikmeot to the boreal–taiga transition zone means that this region likely falls within the northern range limit for a number of both bird and mammal species. This location is also known to harbour vagrants, such as Townsend's Solitaire (*Myadestes townsendi*; Lamont and Knaggs 2016), and previous suspected breeding of this species was confirmed in 2017 near Behchokǫ̀, approximately 50 km northwest of Yellowknife (L. McLeod pers. comm. 6 July 2017).

Similarly, the vascular plant biodiversity is among the richest in Nunavut, with 14 taxa in Kugluk/Bloody Falls Territorial Park not found elsewhere in the territory (Saarela *et al.* 2017). Beyond aerial surveys for raptors and waterfowl (Bromley and McLean 1986; Shank 1996; Conant *et al.* 2007; Lamont *et al.* 2016, 2018), possibly no formal efforts have been made to document passerine diversity. Given that my observations were all collected in a highly localized area, with most travel on foot, more intensive surveys would likely yield additional species previously unrecorded for the region or, potentially, the territory. Those conducting surveys in Nunavut should submit their observations to eBird (www.ebird.com) as recommended by Environment and Climate Change Canada to help define breeding ranges or species previously unknown to breed in the territory.

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SUPPLEMENTARY MATERIAL:

FIGURE S1. Female American Wigeon (*Anas americana*) with young brood on a small pond near Kugluktuk.
FIGURE S2. Female Mallard (*Anas platyrhynchos*) with duckling at edge of small pond near Kugluktuk.
FIGURE S3. Northern Shoveler (*Anas clypeata*) nest found in a sedge meadow near Kugluktuk.
FIGURE S4. Green-wing Teal (*Anas carolinensis*) duckling near Kugluktuk.
FIGURE S5. Greater Scaup (*Aythya marila*) nest in a sedge meadow near Kugluktuk.
FIGURE S6. Says Phoebe (*Sayornis saya*) nest under rock overhang near Kugluktuk.
FIGURE S7. Juvenile Canada Jay (*Perisoreus canadensis*) near Melville Creek south of Kugluktuk.
FIGURE S8. Recently fledged Grey-cheeked Thrush (*Catharus minimus*) near Melville Creek, south of Kugluktuk.
FIGURE S9. Male Yellow-rumped Warbler (*Setophaga coronata*) with recently fledged juvenile, Kugluk/Bloody Falls Territorial Park south of Kugluktuk
FIGURE S10. Dark-eyed Junco (*Junco hyemalis*) carrying insects near Melville Creek, south of Kugluktuk.
FIGURE S11. Bohemian Waxwing (*Junco hyemalis*) seen within the hamlet of Kugluktuk in June 2018.
FIGURE S12. A male Pine Grosbeak (*Pinicola enucleator*) singing near Melville Creek, south of Kugluktuk.

Note

First record of Commander Skate (*Bathyraja lindbergi*) in Canadian Pacific waters

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Abstract

We report the first verified record of a Commander Skate (*Bathyraja lindbergi* Ishiyama and Ishihara, 1977) from British Columbia, Canada. A female measuring 829 mm in total length was captured by bottom trawl on 2 August 2009 in Queen Charlotte Sound, Canada (51°37'N, 130°6'W). The depth of capture was 449 m. We used physical characteristics as well as meristic and morphometric characters to identify the specimen as a Commander Skate.

Key words: Commander Skate; *Bathyraja lindbergi*; British Columbia; first record; range extension

Commander Skate (*Bathyraja lindbergi* Ishiyama and Ishihara, 1977) was described based on several specimens captured in the Bering Sea at depths between 160 m and 570 m. The species is found throughout the Bering Sea southward from approximately 60°N (Ishiyama and Ishihara 1977; Mecklenburg *et al.* 2002); in the eastern North Pacific throughout the Aleutian Islands and in the Gulf of Alaska as far south as the Alexander Archipelago (Stevenson *et al.* 2007); and in the western North Pacific along the Kamchatka Peninsula (Ishiyama and Ishihara 1977) into the Sea of Okhotsk near Hokkaido (Masuda *et al.* 1984). It is found in waters ranging in depth from 126 m to 1193 m (Stevenson *et al.* 2007), but usually deeper than 200 m (Mecklenburg *et al.* 2002). A record reported at a depth of 2000 m is based on an erroneous species identification (Mecklenburg *et al.* 2002). Because of its deep-water habitat, Commander Skate is encountered infrequently in commercial fisheries; for example, from 2004 to 2008, only 100 kg of Commander Skate were recorded by observers as annual bycatch in United States Gulf of Alaska groundfish fisheries (Stevenson and Lewis 2010).

Commander Skate, like all members of the softnose skate family Arhynchobatidae and especially the genus *Bathyraja*, has a soft, flexible snout. In addition, Commander Skate has a short, broad snout and is differentiated from other sympatric species of *Bathyraja* by the absence of scapular thorns and the presence of a continuous row of well-developed, mid-dorsal thorns from the scapular region to the first dorsal fin (Ishiyama and Ishihara 1977).

On 2 August 2009, a Commander Skate was captured by bottom trawl during a research survey conducted on the *M.V. Viking Storm* in Canadian Pacific waters at 51°37'N, 130°6'W. The modal depth of the fishing event was 449 m. The specimen (Figure 1) was a female with a total length of 829 mm, a size at about which 50% of females are mature (Ebert 2005). Initial species identification was based on Stevenson *et al.* (2007), namely: flexible and short snout; scapular thorns absent; median tail thorns well developed along entire length of tail; dorsal surface grey-brown in colour, with ventral surface grey and darker around pectoral and pelvic fin margins; white colour around mouth and nostrils; ventral surface of disc smooth and without denticles; mid-dorsal thorns present and strong. Some authors consider the closely related species *Bathyraja matsubarai* to be a synonym for Commander Skate (Mecklenburg *et al.* 2002), which has contributed to confusion regarding this species' depth range and geographic distribution. *Bathyraja matsubarai* is dark purplish brown in colour and has an interrupted row of mid-dorsal thorns (Ishiyama and Ishihara 1977); neither characteristic applies to our specimen.

The specimen was frozen at sea and thawed later in the laboratory for character counts and measurements according to Hubbs and Ishiyama (1968) and Ishiyama and Ishihara (1977; Table 1). A muscle tissue sample was preserved in 95% undenatured ethanol for genetic analyses. The whole specimen was transferred to the Royal British Columbia Museum (Victoria, British Columbia, Canada) ichthyology collection for long-term storage (catalog number: RBCM 16401). As such, character measurements that required dissection (i.e., spiral valves of the intestine, eyeball length, length of electric organ, and cranium size) were not made. Radiographs were used for vertebral counts, but were not suitable for other measurements of internal structures, such as cranium size.

All character counts and measurements of this specimen were within the range of those made for the holotype (male) and paratypes ($n = 6$ males, $n = 5$ females) of *B. lindbergi* provided in Ishiyama and Ishihara (1977; Table 1). Our specimen is the first record of *B. lindbergi* in Canadian Pacific waters and extends the verified range of this species southward in the eastern North Pacific to include Queen Charlotte Sound, Canada.

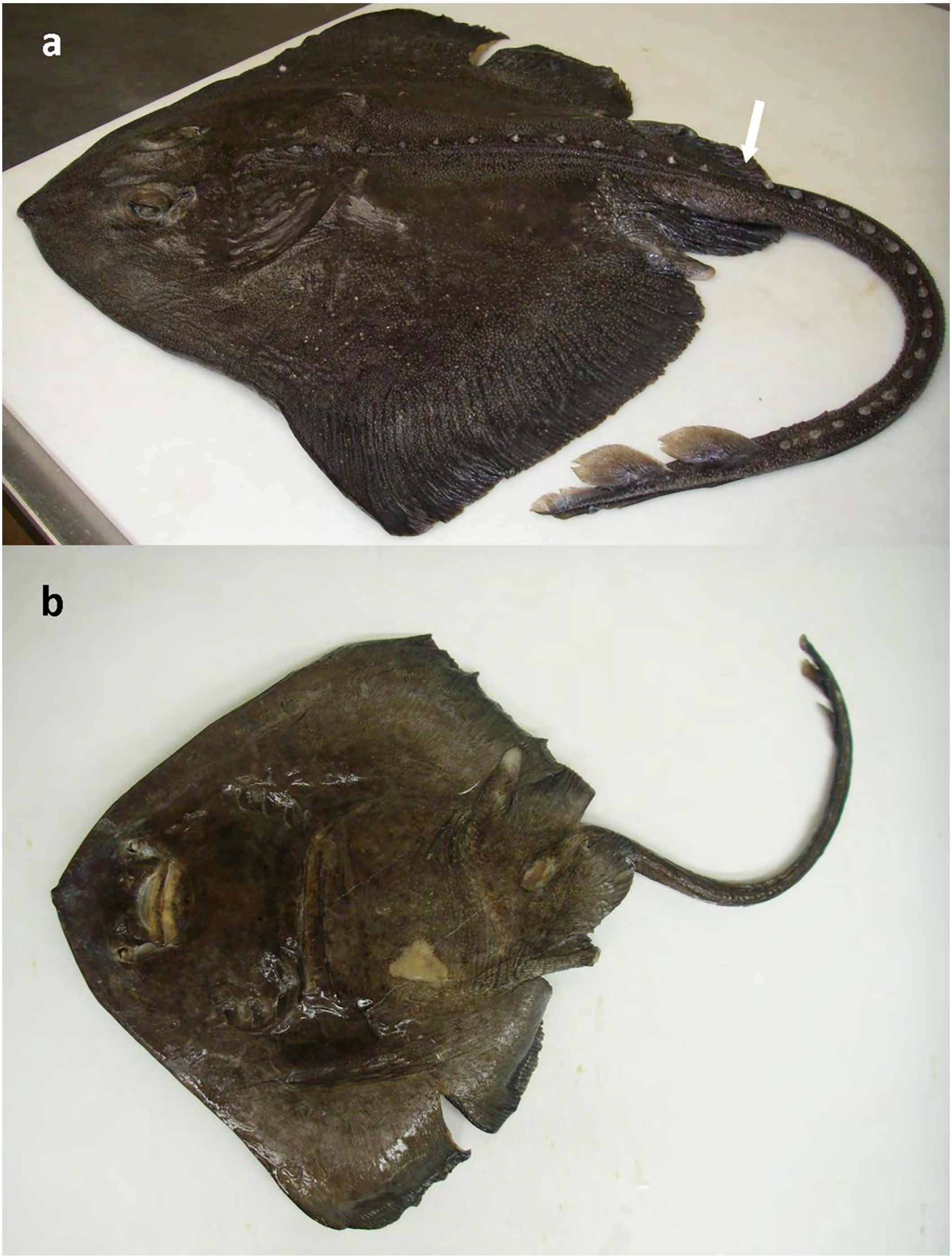

FIGURE 1. Commander Skate (*Bathyraja lindbergi*) collected 2 August 2009 in Queen Charlotte Sound, Canadian Pacific waters (RBCM 16401). a. Dorsal surface with grey-brown colouration; scapular thorns absent; mid-dorsal thorns present and strong; median tail thorns also strong along entire length of tail. Arrow indicates location of one broken thorn evident in pelvic region; base of thorn was intact. b. Ventral surface with grey colouration, darker around pectoral and pelvic fin margins; white colour surrounding mouth and nostrils; ventral surface of disc smooth and without denticles. Photos: T. Zubkowski.

TABLE 1. Character counts and measurements of Canadian Commander Skate (*Bathyraja lindbergi*) specimen collected in Canadian waters (RBCM 16401) along with those reported for the holotype (MTUF 21820) and paratypes (minimum–maximum range) reported in Ishiyama and Ishihara (1977).

Character	Holotype ♂	Paratypes (*n* = 11)	Canadian specimen ♀
Total length, mm	874	768–876	829
Disk width, mm	551	491–607	516
Head length, mm	134	131–153	140
Tail length, mm	482	391–488	437
Precaudal vertebrae	31	29–34	32
Caudal vertebrae	71	68–72	70
Total vertebrae	114	113–117	114
Nuchal thorns	4	3–5	4
Lumbar thorns	5	4–6	6
Tail thorns	25	20–28	23
Tooth rows on upper jaw	27	21–29	26
Pseudobranchial folds	17.5	15–17.5	16
As % of disk width			
Total length	158.6	144.3–160.7	160.7
Disk length	76.8	74.9–81.0	80.4
Tail length	87.5	79.3–88.0	84.7
As % of head length			
Preocular length	59.7	58.8–64.9	64.3
Interorbital length	29.1	23.5–27.0	27.4
Eyeball length	22.4	16.5–20.7	20.0
Spiracle length	22.4	17.3–21.4	19.2
Over first gill slits (female)	–	119.0–133.6	129.3
Eyeball length as % of			
Interorbital length	76.9	67.5–82.4	73.0
Preocular length	37.5	27.1–32.9	31.1
Spiracle length	100.0	83.3–113.8	104.2
As % of tail length			
Precaudal length	81.5	79.1–98.7	89.2
First dorsal fin origin to tail end	24.9	21.4–26.8	24.3
Post dorsal length	7.9	6.6–9.7	8.0

Author Contributions

Writing – Original Draft: J.K.; Writing – Review & Editing: J.K, G.M., and T.Z.; Investigation: J.K., G.M., and T.Z.; Formal Analysis: J.K. and G.M.

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Note

A Canadian range extension for Wormslug (*Boettgerilla pallens*; Gastropoda: Stylommatophora: Boettgerillidae)

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Catling, P.M., and B. Kostiuk. 2018. A Canadian range extension for Wormslug (*Boettgerilla pallens*; Gastropoda: Stylommatophora: Boettgerillidae). Canadian Field-Naturalist 132(3): 264–267. https://doi.org//10.22621/cfn.v132i3.1993

Abstract

The introduced Wormslug (*Boettgerilla pallens* Simroth, 1912) is reported from Quebec, Canada, for the first time, from two closely situated localities in Gatineau Park. It was previously reported from the Vancouver area of British Columbia and, very recently, from Newfoundland. Within the Americas, the species has been reported from northern California, Mexico, and Colombia, and, because it is easily overlooked, likely occurs elsewhere in North America, especially in the eastern United States. In Quebec, it was found in a natural Sugar Maple (*Acer saccharum* Marshall) woodland and an ornamental garden. Wormslug likely reached both sites with shrub plantings from commercial nurseries, probably quite recently, because the invasive spread of the species, worldwide, has occurred mostly during the last few decades. Although the woodland where it occurred is dominated by native plants, the gastropod fauna there is mainly introduced. Identification, characteristics, and ecology of Wormslug are discussed. The potential for impact on native soil and soil surface organisms, including native terrestrial slugs and snails, is noted.

Key words: Wormslug; *Boettgerilla pallens*; Quebec; introduced; invasive; slug; spread; distribution; ecology

During a general biodiversity reconnaissance in Gatineau Park, Quebec, in September and October 2017, we discovered two closely situated occurrences of Wormslug (*Boettgerilla pallens* Simroth, 1912). This largely subterranean, worm-like slug (Figure 1), which is native to southeastern Europe, has expanded its range remarkably over the past few decades (e.g., Kerney 1999; Reise *et al.* 2000; Maunder *et al.* 2017). The newly discovered populations in Quebec are ~3500 km east of previous known occurrences in the Vancouver area of British Columbia (Reise *et al.* 2000) and ~1790 km west of a recently reported occurrence in Newfoundland (Maunder *et al.* 2017). The nearest known United States location is in northern California (McDonnel *et al.* 2014), ~3800 km to the west. It is an easily overlooked species and likely occurs elsewhere in North America, particularly in the eastern United States.

Only two species of *Boettgerilla* are known, both originating in the Caucasus Mountains, east of the Black Sea. *Boettgerilla pallens* may also be native in the relatively nearby mountains of Crimea (Balashov and Baidashnikov 2012). Although *B. pallens* has expanded its world range dramatically during the last century, *Boettgerilla compressa* Simroth, 1910 has not yet been reported from outside of the southwestern Caucasus Mountains (Sysoev and Schileyko 2009). *Boettgerilla compressa* differs (Sysoev and Schileyko 2009) from *B. pallens* in that the adults are ~20 mm long when contracted instead of 10 mm long, pale brownish-yellow instead of pale grey, and laterally compressed across the back (hence the name) instead of equilaterally triangular (Simroth 1912: 121) to somewhat cylindrical. Although our specimens seem best placed with *B. pallens*, and that is the species associated with all records of range expansion, we note that the distinctive features are size and age-related, and that *B. compressa* may benefit from additional taxonomic study.

The only other slug present in the general Gatineau Park region of Quebec that is likely to be confused with *B. pallens* is the pale greyish Pale Mantleslug (*Pallifera dorsalis* (A. Binney, 1842)). The latter differs in being shorter when extended, in lacking a keeled tail, and in having a rounded mantle that extends almost to the tip of the tail. *Boettgerilla pallens* is very slender and has a keel on the back half of its body extending from behind the mantle to the tip of the tail. In addition, the mantle has a different texture with concentric ridges (Figure 1a,b) and tapers to a broad point distally.

The adult Wormslugs found at the Meech Lake site in Gatineau Park were 20–45 mm long and 2–3 mm wide when extended. Most were light greyish with the front of the head, front of the mantle, keel, and tip of the tail being darker grey (Figure 1a). Two of the longest individuals, both 45 mm when extended, were a darker grey overall and had some brownish colouring (Figure 1b). Individuals that we thought likely to be juvenile were ~20 mm when extended and mostly white with yellowish internal organs visible through the whitish translucent body (Figure 1d). Size and colour are age-related in *B. pallens*, with "juveniles" being distinctly whitish (Gunn 1992; Rowson *et al.* 2014).

When picked up with forceps (or otherwise irritated) the body behind the mantle compressed laterally, becoming 1 mm thick in dorsal view (and 4 mm wide in

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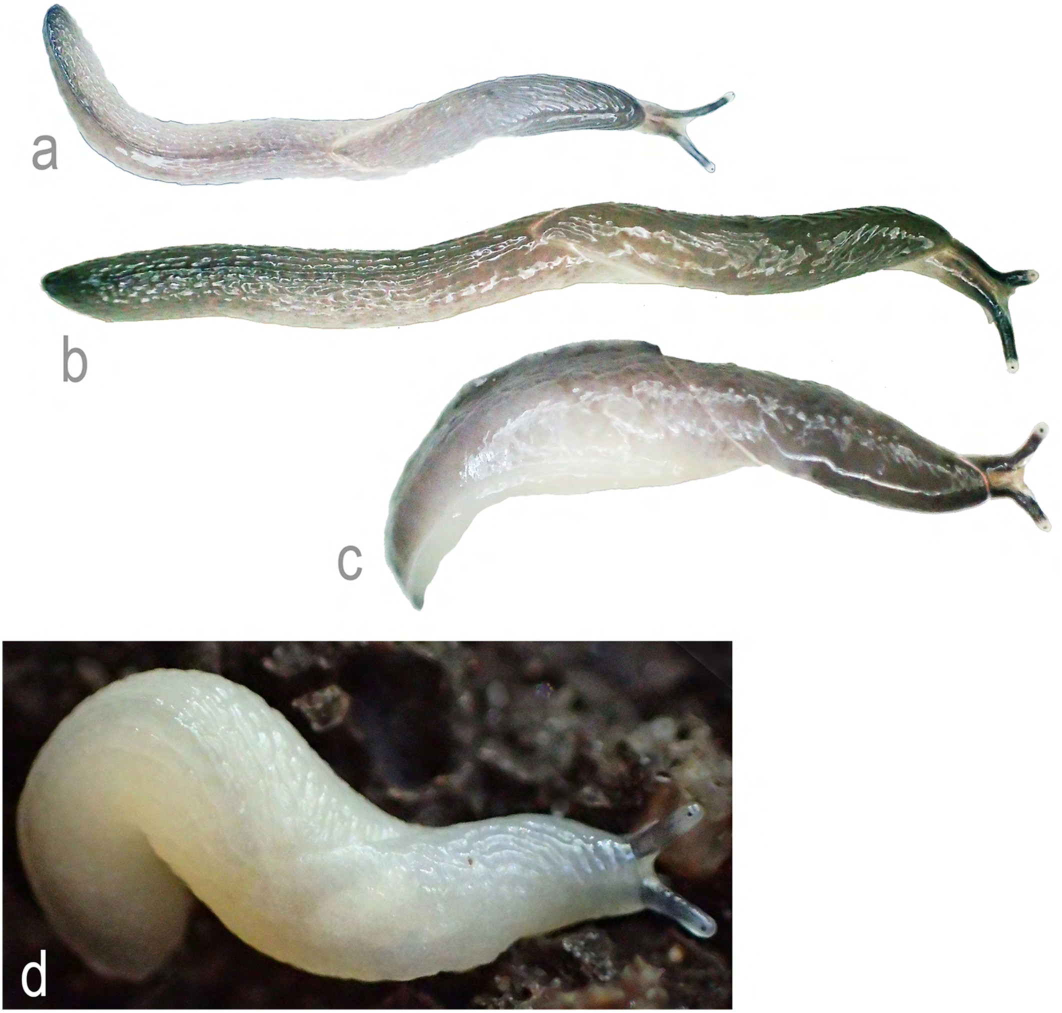

FIGURE 1. Wormslugs, *Boettgerilla pallens*, from Meech Lake, Gatineau Park, Quebec. a. Mostly pale grey and 30 mm when extended. b. Darker and brownish and 45 mm when extended. c. Same individual as b but with back half laterally compressed and keel raised as a thin, long dorsal fin. d. A whitish and semi-transparent juvenile Wormslug showing internal organs; the animal was 20 mm in length when extended. Photos: P.M. Catling and B. Kostiuk.

lateral view), and the keel became prominently raised (Figure 1c). When the head was touched, it withdrew under the mantle which extended and flattened or folded over the head like an envelope so that its sides met.

A number of illustrations are available in addition to our photographs (Figure 1) to assist in identification including Simroth (1912: Plate 3, Figure 50, Plate 8, Figure 32), Wiktor (1959: Figures 6 and 7, 1961: Figures 3–5), Reise *et al.* (2000: Figure 1), Barker and Efford (2004: Figure 6.8), Grimm *et al.* (2009: Plate 1), Sysoev and Schileyko (2009), Balashova and Baidashnikov (2012: Figure 1b), and Maunder *et al.* (2017: Figures 1–4).

Since expanding its range from its native Caucasus Mountains, apparently during the last 100 years, *B. pallens* has been reported from much of central and western Europe, ranging north to Scandinavia (Kerney and Cameron 1979; Reise *et al.* 2000; Eversham 2012; Anderson 2016; Maunder *et al.* 2017). It is also known from the Canary Islands (Margry 2014). In the Americas, it has most recently been discovered in St. John's, Newfoundland (Maunder *et al.* 2017). Additional occurrences have been reported from southwestern British Columbia (Reise *et al.* 2000; Grimm *et al.* 2009; Maunder *et al.* 2017), California (McDonnell *et al.* 2014), Mexico (Araiza-Gómez *et al.* 2016), and Colombia (Hausdorf 2002).

In its introduced range, *B. pallens* occupies anthropogenic habitats, including gardens, greenhouses, semi-wild city parks, and plant nurseries. However, in the

Americas, in particular, it also occupies a number of "natural-looking habitats" (Maunder *et al.* 2017). It is said to have successfully penetrated forests and other natural habitats in recently colonized parts of Europe (Grimm *et al.* 2009).

At the Meech Lake, Gatineau Park site, the habitat where it was found is mesic woodland dominated by Sugar Maple (*Acer saccharum* Marshall) and Eastern White Cedar (*Thuja occidentalis* L.). Prominent herbs included: Blue-stemmed Goldenrod (*Solidago caesia* L.), Common Lady Fern (*Athyrium filix-femina* (L.) Roth ex Mertens), Drooping Woodland Sedge (*Carex arctata* Boott), Interrupted Fern (*Osmunda claytoniana* L.), Large False Solomon's Seal (*Maianthemum racemosum* (L.) Link subsp. *racemosum*), Lindley's Aster (*Symphyotrichum ciliolatum* (Lindley) Á. Löve & D. Löve), and Tall Rattlesnakeroot (*Nabalus altissimus* (L.) Hooker). This habitat is in a valley where a small stream cascades over granite boulders at the base of a steep north-facing slope.

These Wormslugs were found ~20–70 m along a trail from the parking area into natural forest. Although the forest showed no signs of recent disturbance, it was apparently subject to domestic cutting a little more than 100 years ago. The landscape may have been much more open at that time, as a consequence of this wood cutting. Although the habitat now appears essentially natural, the only terrestrial snails present (observed in a 1-h search in an area of 0.40 ha) were: the possibly introduced locally (Holarctic) Glossy Pillar (*Cochlicopa lubrica* (Müller, 1774); *n* = 7); possibly introduced (Holarctic) Black Gloss (*Zonitoides nitidus* (Müller, 1774); *n* = 3); and native Quick Gloss (*Zonitoides arboreus* (Say, 1817); *n* = 6). The slugs present were all introduced including Garden Arion (*Arion hortensis* Férussac 1819, *sensu lato*; *n* = 50); Dusky Arion (*Arion subfuscus/fuscus* (Draparnaud, 1805); *n* = 1); and Grey Fieldslug (*Deroceras reticulatum* (Müller, 1774); *n* = 5).

At the Old Chelsea Picnic Area site, also in Gatineau Park, the habitat where the Wormslugs were found was an ornamental garden dominated by a variety of planted perennials including: Variegated Goutweed (*Aegopodium podagraria* L.), daylilies (*Hemerocallis* spp.), geraniums (*Geranium* spp.), Eastern Purple Coneflower (*Echinacea purpurea* (L.) Moench), and Eastern White Cedar (*Thuja occidentalis* L.). This garden is more than 20 years old and has undergone many recent changes including additions of plants and rearrangement of paths. The terrestrial gastropod fauna (observed in a 0.5-h search in an area of ~0.10 ha) is mostly introduced, including: possibly introduced (Holarctic) Glossy Pillar (*n* = 2); introduced Hairy Hellicid (*Trochulus hispidus* (L., 1758)); *n* = 3); possibly introduced (Holarctic) Black Gloss (*n* = 1); and introduced Garlic Glass-snail (*Oxychilus alliarius* (Miller, 1822); *n* = 1). The slugs present were: the introduced Grey Fieldslug (*n* = 15); and native or possibly introduced (Holarctic) Meadowslug (*Deroceras laeve* (Müller, 1774); *n* = 1).

All these Wormslugs were found under rocks or logs more or less buried in the soil. This species is known to use earthworm burrows (Gunn 1992; Shikov 2007) and we found them in rodent burrows, as well as other spaces in soil and debris. They have been reported to descend to 60 cm below the soil surface (Gunn 1992). Earthworms (all introduced) were frequent at both Gatineau Park sites, and there were no accumulations of decomposing leaf litter at either site, so no litter samples were collected or available to search for minute snail species.

Wormslugs typically spread by transport in soil associated with cultivated plants (Reise *et al.* 2000). In 1900, the Meech Lake site was part of the Blanchet Farm where pears, plums, and apples had long been introduced. Along the southern shore of Meech Lake, there are currently many cottages with plantings of introduced perennials, shrubs, and trees in rock gardens. These plantings were probably built up throughout the last century judging by the age of some cottages. Within the last two decades, the Blanchet homesite was converted into a parking lot for beach access, and various shrubs were planted around it, including Red-osier Dogwood (*Cornus sericea* L.), Rugosa Rose (*Rosa rugosa* Thunberg), and Nannyberry (*Viburnum lentago* L.). Although some of the planted shrubs are native, they all likely originated from commercial nurseries potentially harbouring non-native gastropods. The Chelsea site has perennials that were probably introduced from one or more commercial nurseries that also probably had populations of introduced gastropods (as all local nurseries do). Thus both occurrences are consistent with the general explanation for the spread of Wormslugs.

These burrowing slugs are said to feed on fungi, micro-organisms, roots, decaying vegetation, eggs of other gastropods, and possibly invertebrates (Barker and Efford 2004; Eversham 2012). They are also reported to appear at the surface at night and feed on medium-sized snails (Shikov 2007). Unlike many other slugs, they are said not to survive in captivity on oatmeal, mushrooms, and carrot (Eversham 2012). Although Wormslug has not definitely been implicated as an agricultural pest, there does seem to be a potential for impact on native soil and soil surface organisms including native terrestrial snails. It may spread rapidly as appears to be the case following initial detection elsewhere (e.g., Eversham 2012).

Voucher specimens

Canada, Quebec: Gatineau Park: North-facing slope at the west end of Meech Lake above the Blanchet homestead parking area at the start of Sentier des Loups, 45.5425°N, 75.9107°W, Sugar Maple woods by stream, 20 September 2017, *P.M. Catling 2017120 and B. Kostiuk*, two specimens preserved of eight – Canadian Museum of Nature (CMNML 2018-1704). Old Chelsea Picnic Area, 45.5012°N, 75.8128°W, ornamental garden, 9 October 2017, *P.M. Catling 2017148 and B. Kostiuk*, one specimen preserved of three – Canadian Museum of Nature (CMNML 2018-1703).

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Spring food habits of Wolverine (*Gulo gulo*) in the Colville River watershed, Alaska

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Abstract

Wolverines (*Gulo gulo*) are relatively abundant on the North Slope of Alaska, an Arctic ecosystem dominated by tundra habitats that run north from the Brooks Range across a wide coastal plain to the Beaufort Sea. The region contains a range of potential Wolverine prey species, including ungulates (Caribou [*Rangifer tarandus*], Moose [*Alces americanus*]), Arctic Ground Squirrel (*Urocitellus parryii*), and both Soricidae and Cricetidae species. The seasonal composition of these, and other prey species, in the Wolverines' diet is not well understood. We collected Wolverine scats during spring (March–May) on the North Slope while tracking animals from snowmobiles and with helicopters that visited areas identified as of interest during ground surveys or using global positioning system collared animals. We analyzed prey remains in 48 scat samples based on hair, bone, and other prey fragments. We then calculated frequency of occurrence, percentage of occurrence, and weighted percent volume for each major prey category detected. We confirmed species identity of scats as Wolverine by amplifying the control region of the mitochondrial DNA. We estimated spring diet diversity and richness based on nine major prey categories detected in scats. Ungulates and cricetids together constituted 69% of the Wolverines' spring diet, with Snowshoe Hare (*Lepus americanus*) constituting 9%, fox (*Vulpes* spp.) 6%, Arctic Ground Squirrel 2%, birds 2%, American Beaver (*Castor canadensis*) less than 1%, and unknown 6%.

Key words: Wolverine; *Gulo gulo*; diet; food habits; frequency of occurrence; percentage of occurrence; volume of occurrence; diet richness; diet diversity; Alaska

Introduction

Wolverines (*Gulo gulo*) are known as "facultative scavengers" that alternate between hunting live prey, scavenging, and consuming previously cached food to fulfill their energy requirements (Magoun 1987; Banci 1994; Dijk *et al.* 2008; Dalerum *et al.* 2009; Koskela *et al.* 2013; Mattisson 2016). In the Arctic, Wolverines generally switch from killing and consuming cached ungulate carrion (e.g., Caribou [*Rangifer tarandus*]) in the winter, to hunting small mammals (e.g., Arctic Ground Squirrel [*Urocitellus parryii*]) during the summer (Magoun 1987; Dijk *et al.* 2008). Because habitat and prey species availability differ across the Arctic and across seasons, Wolverines likely adjust their diet according to available prey sources (Churchill 1955; MacDonald and Cook 2009; Lenart 2015). Variation of diet composition may reflect prey availability, which in turn may influence the distribution and abundance of Wolverines. In this study, we focus on spring diet composition during the transition from winter to summer, defined here as March through May, in the Colville River watershed of the Alaskan Arctic.

Across their range, Wolverines feed on a variety of prey species comprised primarily of ungulates (Moose [*Alces americanus*], Caribou) in North America and Europe (Landa *et al.* 1997; Dalerum *et al.* 2009; Koskela *et al.* 2013; Inman and Packila 2015). However, Wolverines also forage on small mammals, birds, and fish (Magoun 1987; Landa *et al.* 1997; Samelius *et al.* 2002; Shardlow 2013; Inman and Packila 2015). In the North American Arctic, in addition to ungulates, Wolverines feed on ptarmigan (*Lagopus* spp.), soricids (shrews), cricetids (voles, lemmings, mice), hare (*Lepus* spp.), and Arctic Ground Squirrels (Banci 1987; Mulders 2001). One study conducted on Alaska's North Slope investigated the Wolverines' seasonal diet composition in summer (May–August) and winter (September–April) near the Utukok River in the foothills of the Brooks Range, and found that Wolverines relied heavily on Arctic Ground Squirrel almost the entire year, except in midwinter (December–February) when their diet shifted to Caribou (Magoun 1987). Caribou undertake seasonal migrations and Moose reside at low densities on the North Slope of Alaska (Fancy *et al.* 1989; Carroll 2014; Tape *et al.* 2016), suggesting that Wolverines may need to rely on cached food or alternative prey sources when ungulates are scarce.

Information on the relative contribution of small prey such as cricetids, soricids, Snowshoe Hare (*Lepus americanus*), ptarmigan, and large prey in the Wolverines' diet across the Alaskan Arctic is lacking, but could contribute towards understanding how prey selection influen-

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ces Wolverine survival and reproductive success (Krebs *et al.* 2004; Persson 2005; Koskela *et al.* 2013). A lack of large ungulate prey coupled with dwindling food caches during early spring may force Wolverines to switch from ungulate carrion to other prey sources (Persson 2005). Investigating the relative presence of large versus small mammals (Cricetidae, Soricidae, Sciuridae, Leporidae) in the Wolverines' spring diet is an important step in understanding how Wolverines in the Arctic address a period of high energetic demands (Magoun 1987; Landa *et al.* 1997; Dalerum *et al.* 2009).

We collected Wolverine scats on the North Slope near Umiat, Alaska to determine spring diet composition of Wolverines in the foothills of the Brooks Range and Beaufort coastal plain (Figure 1). Our objectives were to describe the spring diet composition of Wolverines in our study area and compare the portion of that period's diet made up of small mammals versus ungulate prey.

Study Area

Our study took place in 2016 within 120 km of Umiat, Alaska in the National Petroleum Reserve-Alaska (NPR-A; Figure 1). On the southeast border of the NPR-A lies the Colville River corridor made up of flood plain with shrubs such as alder (*Alnus* spp. Miller) and willow (*Salix* spp. L.). Northwest of the Colville River are rolling hills with steep cut drainages, composed of upland tundra vegetation such as Tussock Cottongrass (*Eriophorum vaginatum* L.) and mountain avens (*Dryas* spp. L.; Viereck *et al.* 1992). Further north, the land transitions from rolling hills to a flattened terrain filled with lakes and ponds, which extends north to the coast of the Beaufort Sea. This area is considered lowland tundra, containing Water Sedge (*Carex aquatillis* Wahlenberg) and other mesic plant species (Churchill 1955). At Umiat, average temperatures range from −30°C in February to 13°C in July (NOAA 2018). Average annual rain and snow accumulation are 13.9 cm and 84.3 cm, respectively.

While large ungulates, cricetids, soricids, other small mammals (e.g., Snowshoe Hare, Arctic Ground Squirrel), and birds are available as prey to Wolverines during spring (Table 1), their relative abundance may change over time and space (MacDonald and Cook 2009). Caribou are seasonally available as they migrate through the study area in spring and fall, residing near the coast in summer, and in the Brooks Range to the south in winter (Lenart 2015). Moose and Muskox (*Ovi-*

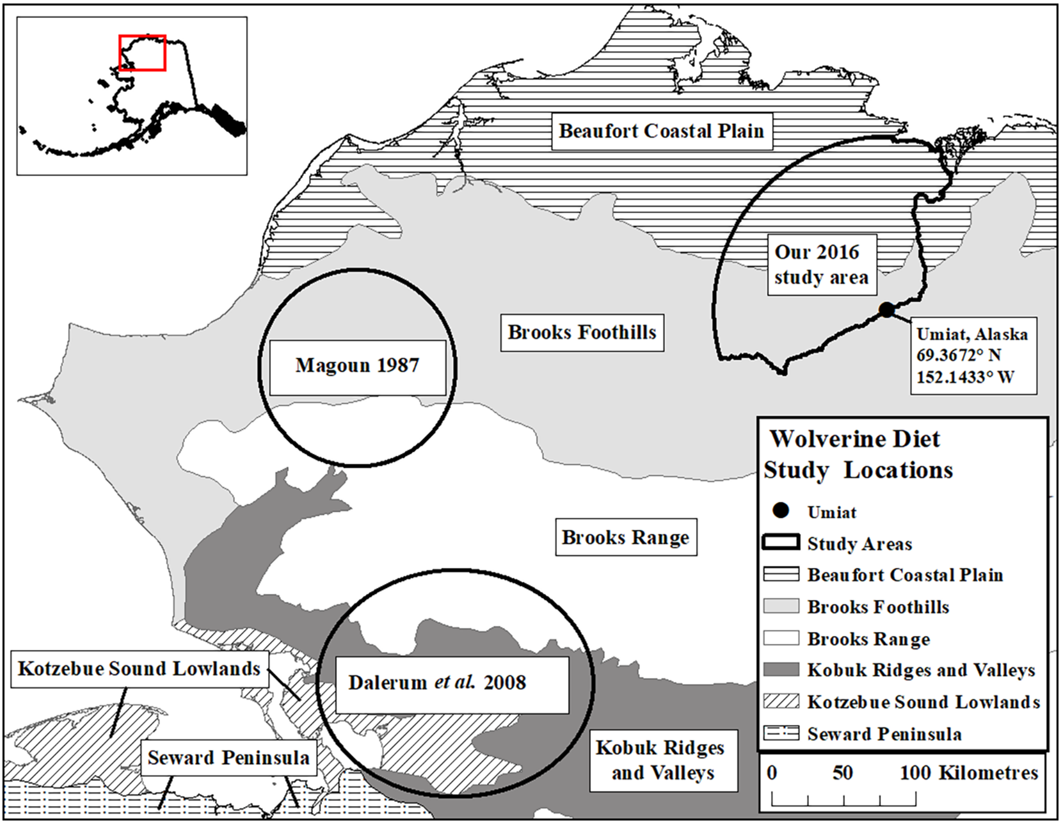

FIGURE 1. Wolverine (*Gulo gulo*) diet study areas compared to the ecoregions of northern Alaska, USA. Our 2016 study area took place within 120 km of Umiat, Alaska in the National Petroleum Reserve-Alaska.

bos moschatus) persist at low densities year-round, but Muskox only inhabit the northern portion of the study area near the Beaufort Sea (MacDonald and Cook 2009; Carroll 2014). Smaller prey that inhabit the study area year-round include: cricetids, soricids, Arctic Ground Squirrel, Snowshoe Hare, Willow Ptarmigan (*Lagopus lagopus*), and Rock Ptarmigan (*L. muta*; MacDonald and Cook 2009). Cricetids and soricids are active underneath the snow year-round, while Arctic Ground Squirrels hibernate, reducing the Wolverines access to these species in winter and early spring (Batzli and Sobaski 1980). In contrast, Snowshoe Hare and ptarmigan are available year-round. Wolverines are known to cache their prey, thus any species listed above may be consumed during winter and spring (Magoun 1987).

Methods

Scat collection

We followed Wolverine tracks by snowmobile 10 March–29 April 2016 to collect scats for diet analysis. We followed tracks opportunistically while maintaining a live-capture trap line, picking up scats from unknown individuals. When we encountered relatively fresh Wolverine tracks (e.g., not blown over, or covered with snow), we followed the track against the direction of travel to avoid harassing the animal. If tracks were older (e.g., blown over with snow) we followed the track in either direction. We stopped tracking when the animal travelled through terrain unnavigable by snowmobile, or when tracking conditions deteriorated. We recorded global positioning system (GPS) coordinates for each scat collected. We recorded the location of Wolverine snow-holes encountered while tracking and returned to collect scats in late spring after the snow melted. At carcass sites, we collected all scats, but only included one randomly selected scat in our analysis to avoid pseudoreplication and the over-representation of the prey species at the carcass site (Marucco *et al.* 2008; Bacon *et al.* 2011).

We captured five Wolverines 6–26 April 2016 and affixed GPS collars (Tellus light model, Followit Sweden AB, Lindesberg, Sweden) programmed to record locations every 20 minutes. We captured three females including one juvenile and two reproductive females (with kits), one juvenile, and an adult male. Collars remained on animals until mid-summer when drop-off mechanisms were activated. In addition to scats collected while tracking unknown individuals, we collected scats from areas where collard Wolverines spent >20 minutes in an area <100 m^2, signifying an extended stay in a localized area where scat could be found (called a cluster). We returned to snow-holes and clusters on 29 May to collect scats.

We placed scats in Whirl-Packs® (Nasco, Fort Atkinson, Wisconsin, USA) and stored them at temperatures ranging from 4°C to −35°C while in the field (10 March –29 April, and 29 May). After leaving the field, we stored samples in a −20°C freezer for a maximum of 1.5 months.

We radio-tracked collared Wolverines with fixed-winged aircraft 13–22 May to observe feeding behaviour. We watched for visually identifiable prey (e.g., a

TABLE 1. List of potential prey items available in late winter and early spring to Wolverines within the National Petroleum Reserve-Alaska (MacDonald and Cook 2009).

Family	Common name	Scientific name
Bovidae	Muskox	*Ovibos moschatus*
Canidae	Gray Wolf	*Canis lupus*
	Arctic Fox	*Vulpes lagopus*
	Red Fox	*Vulpes vulpes*
Cervidae	Moose	*Alces americanus*
	Caribou	*Rangifer tarandus*
Cricetidae	Peary Land Collard Lemming	*Dicrostonyx groenlandicus*
	Brown Lemming	*Lemmus trimucronatus*
	Singing Vole	*Microtus miurus*
	Tundra Vole	*Microtus oeconomus*
	Northern Red-backed Vole	*Myodes rutilus*
Felidae	Lynx	*Lynx canadensis*
Leporidae	Snowshoe Hare	*Lepus americanus*
Mustelidae	Wolverine	*Gulo gulo*
	Ermine	*Mustela erminea*
	Least Weasel	*Mustela nivalis*
Phasianidae	Willow Ptarmigan	*Lagopus lagopus*
	Rock Ptarmigan	*Lagopus muta*
Sciuridae	Arctic Ground Squirrel	*Urocitellus parryii*
Soricidae	Cinereus Shrew	*Sorex cinereus*
	Tundra Shrew	*Sorex tundrensis*
	Barren Ground Shrew	*Sorex ugyunak*
	Holarctic Least Shrew	*Sorex minutissimus*
Ursidae	Brown Bear	*Ursus arctos*
	Polar Bear	*Ursus maritimus*

Moose carcass), and observed hunting behaviour (e.g., hunting small prey). We recorded time, location, collared animal's identity, and observed prey or behaviour.

Scat analysis

We confirmed identification of each scat as Wolverine with faecal DNA analysis, because tracking trails and clusters also had sign of other predators (e.g., foxes). We used three methods to sample faecal DNA from each scat. First, we scraped each scat using two flat-sided toothpicks and placed each into a coin envelope. Second, we removed 1 mL of faecal material from each scat and placed it into a vial. Finally, we swabbed each scat with a sterile cotton-tipped swab and placed it into a separate vial. We sent all samples to the Rocky Mountain Research Station, National Genomics Centre for Wildlife and Fish Conservation in Missoula, Montana to verify the species identity. We used the QIAGEN QIAamp Fast DNA Stool Mini Kit (QIAGEN Inc., Valencia, California, USA) following the manufacturer's instructions for DNA extraction. We amplified the control region of mitochondrial DNA (mtDNA) for species identification following Schwartz *et al.*'s (2007) methods for processing samples.

Following DNA sampling, we transferred individual scats into nylon mesh stockings and washed them on gentle cycle in a Haier HLP23E compact washing machine (Haier Appliances, Rapid City, South Dakota, USA). We washed scats for 2–3 cycles until the water ran clear (indicating the removal of the faecal matrix material) and air-dried samples for 48 h. We weighed each scat and identified prey remains by comparing microscopic qualities of medulla, cortex, and cuticular scale patterns of mammalian hairs to published keys (Moore *et al.* 1974; Carlee and Horelick 2011), and by comparing hair, teeth, claw, and bone fragments to reference specimens on loan from University of Alaska Museum of the North, Fairbanks, Alaska. We identified prey remains to species level or nearest taxonomic grouping if remains were highly degraded. We visually estimated the proportion of each prey type present in each scat, rounded to the nearest 5%. We also sub-sampled scats after determining the proportion of the scat belonging to each prey category. Of the scats that contained suspected cricetids and soricids, we collected 15–30 hairs to determine species identification through DNA analysis.

We used methods from Dijk *et al.* (2007) and the recommendations of Klare *et al.* (2011) to characterize Wolverine diet. Frequency of occurrence (FO) was calculated from the binary occurrence of each prey item in each scat, and represents the percentage of the total sample size containing each prey item:

$$FO_i(\%) = \frac{n_i}{N} \times 100$$

where n_i is the number of scats containing species *i* and N represents the total number of scats (Ciucci *et al.* 1996).

Percentage of occurrence (PO) is calculated from binary occurrence data that represents the percentage of the total prey occurrences containing each prey item:

$$PO_i(\%) = \frac{n_i}{\sum n_i} \times 100$$

where n_i is the number of scats containing species *i*. Finally, we calculated weighted volume (VOL) to determine the relative importance of prey in the diet in the absence of a biomass calibration (Klare *et al.* 2011).

Weighted volume is the sum of percent volume of each prey item in scats, divided by the total number of scats:

$$VOL_i(\%) = \frac{\sum v_i}{N} \times 100$$

where v_i is the proportion of each scat containing species *i*.

Scats collected while tracking individual Wolverines were treated as individual sample units. Scats collected from individual snow-holes and clusters were combined and treated as a single sample unit, because the large piles of scats collected at clusters, deposited by an unknown number of individuals, made it difficult to differentiate among individual scat samples. For scats collected at clusters, v_i was equal to the proportion of the total scat volume at a cluster.

Weighted volume was calculated for each prey item detected in scats. We then grouped prey items into one of nine major prey categories and calculated weighted volume of each major prey category in scats. The nine prey categories were: ungulate, Snowshoe Hare, Arctic Ground Squirrel, cricetids and soricids, birds (Aves), fox, American Beaver, unknown (including any unidentifiable remains), and other (consisting of vegetation, gravel, and woody debris). Items in the "other" category were expected to be incidentally ingested as a result of digging up food caches or excavating small mammal burrows. Although Wolverines have been documented to consume vegetation and berries, we assumed vegetation was incidentally ingested while feeding (Lofroth *et al.* 2007) or picked up during collection of scats. Thus we dismissed it from our analysis.

We estimated diet richness as the overall number of items in the diet, and diet diversity, which indexes heterogeneity and accounts for relative abundance of each item in the diet (Krebs 1999). We estimated diet diversity using the Shannon-Wiener diversity index (H'), whereby the higher the index value, the more evenness in use across all resources:

$$H' = \sum \hat{\rho}_i \ln \hat{p}_i$$

where p_i is the total proportion of species *i* in the sample (Colwell and Futuyma 1971). We estimated 95% CI for diet richness, diversity, and volume of each of the nine major prey categories based on 1000 bootstrap re-samplings of scat data (Manly 2006).

We used rarefaction to assess how diet diversity and richness varied with sample size (Krebs 1999). Rarefaction uses bootstrap resampling techniques to subsample from the initial dataset (without replacement) and estimate the mean and variance of the desired index (e.g., diversity, richness) for each sample size, *n*, from one to the maximum number of scat samples. We generated rarefaction curves based on 1000 bootstrap runs. Diet indices and bootstrapping and rarefaction analyses were calculated in Program R v 3.0.1 (R Development Core Team 2014).

Results

Scat collection

We collected 104 scat samples while tracking individual Wolverines from 10 March to 29 April (*n* = 83) and first visited GPS-identified clusters on 29 May (*n* = 22; Figure 2). We followed 64 km of tracks, collecting 83 scats during 30 tracking events. We collected 21 scats from 20 GPS-cluster sites (14 snow-holes monitored by motion-activated cameras and six clusters detected by GPS collar locations). We also collected 29 scats from near a Moose carcass.

Faecal DNA analysis confirmed 70 of the 104 scats we collected as Wolverine, 23 as Red Fox (*Vulpes vulpes*), three as Arctic Fox (*Vulpes lagopus*), and eight with poor DNA quality that precluded identification. Of the 29 scats collected at the Moose carcass, 15 were identified as Wolverine, and we randomly chose one of these scats to include in our analysis (Marucco 2008; Bacon *et al.* 2011). We combined 15 of the scats collected at clusters identified as Wolverine into eight cluster scat samples, for a final sample size of 48 (40 from tracking and eight from GPS-clusters). Of the scats containing cricetids (*n* = 25), three contained Peary Land Collared Lemming (*Dicrostonyx groenlandicus*), two Brown Lemming (*Lemmus trimucronatus*), two Singing Vole (*Microtus miurus*), and others contained hairs that were non-cricetid or had poor quality DNA, preventing species identification. No soricids were found in scats.

Scat analysis

We classified prey remains and scat contents as one of 11 categories, five of which we identified to the species level (Figure 3): unknown ungulate (too degraded to distinguish between Moose or Caribou), Moose, Caribou, unknown carnivore (too degraded to determine species), fox, American Beaver, Snowshoe Hare, Arctic Ground Squirrel, cricetids, birds, and unknown (unidentified bone and other debris). We did not attempt to identify feather remains beyond the "bird" category because the majority of feathers were too highly degraded for species identification, although we expect that they were predominantly ptarmigan based on our

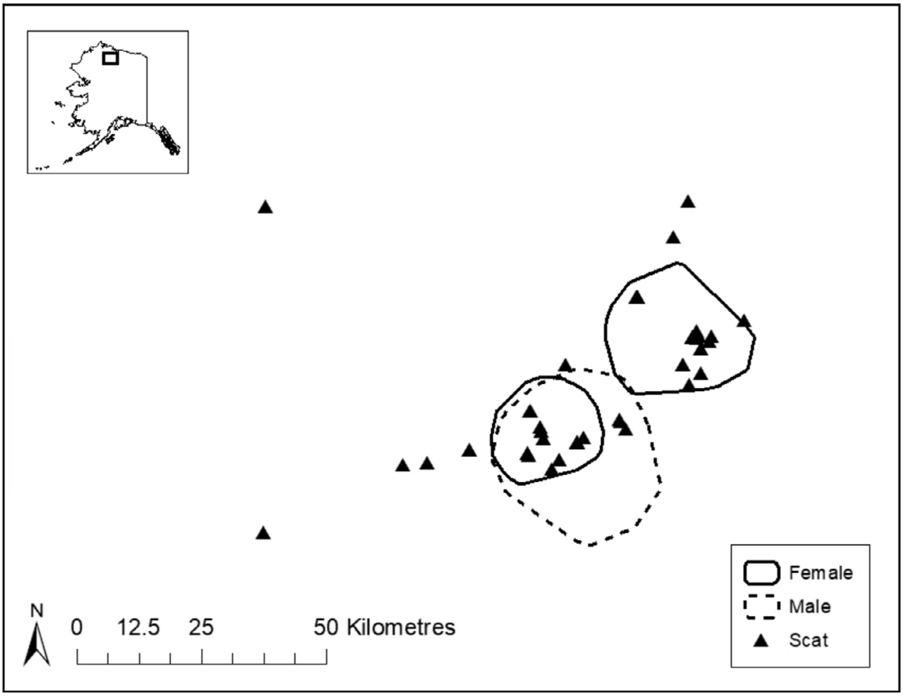

FIGURE 2. Locations of Wolverine (*Gulo gulo*) scats collected and home ranges of three Wolverines (one male, two female) near Umiat, Alaska, USA 10 March–29 April, and 29 May 2016. We collected 67 scats later confirmed through DNA analysis as Wolverine. Home ranges represent 95% minimum convex polygons. Locational details have been purposely omitted.

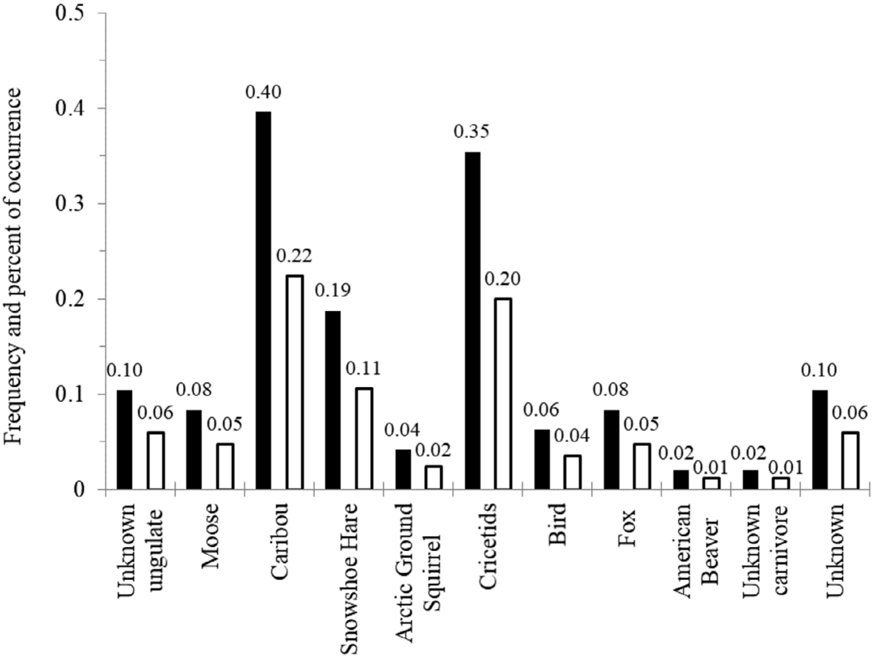

FIGURE 3. Frequency and percent of occurrence (FO and PO, respectively) of all prey species detected in combined Wolverine (*Gulo gulo*) scats ($n = 48$) collected near Umiat, Alaska, USA, 10 March–29 April, and 29 May 2016. Closed bars represent FO and open bars represent PO. Prey detected includes: unknown ungulate (Moose [*Alces americanus*], Caribou [*Rangifer tarandus*]), Moose, Caribou, Snowshoe Hare (*Lepus americanus*), Arctic Ground Squirrel (*Urocitellus parryii*), cricetids (Brown Lemming [*Lemmus trimucronatus*], Peary Land Collared Lemming [*Dicrostonyx groenlandicus*], Singing Vole [*Microtus miurus*]), bird (Aves), fox (Red Fox [*Vulpes vulpes*], Arctic Fox [*Vulpes lagopus*]), American Beaver (*Castor canadensis*), unknown carnivore (Carnivora), and unknown. Vegetation (FO = 0.25, PO = 0.14) and woody debris (FO = 0.06, PO = 0.04) not shown.

observations while in the area and consumption by Wolverines elsewhere.

Raw measures of FO and PO indicated that the four most commonly occurring items in scats were Caribou, cricetids, vegetation (assumed to be incidentally ingested during feeding or scat collection and not considered in further analyses), and Snowshoe Hare (Figure 3). Ranking prey items by volume indicated that the three most abundant identifiable items were Caribou, cricetids, and Snowshoe Hare. Cricetids and Caribou collectively represented 55% volume of the diet (Figure 3). Bootstrapped estimates of volume (mean ± SD) of each of the nine major prey categories indicated that ungulates (0.49 ± 0.07) and cricetids (0.20 ± 0.05) were the two primary prey resources (Figure 4). Arctic Ground Squirrel (0.02 ± 0.03) made a minor contribution to the diet.

Mean diet richness was eight resource categories (8.43 ± 0.81; Figure 5a). Mean Shannon-Wiener diversity index for scats was 1.75 ± 0.11. Rarefaction curves showed that mean diet richness continued to increase up to a sample size of about 40 scats, after which the rarefaction curve began to approach an asymptote (Figure 5a). Rarefaction of mean diet diversity showed that the diversity curve approached an asymptote after a sample size of about 20 (Figure 5b).

We observed five instances of active hunting by Wolverines between 13 and 22 May. Three events were of an adult male and two events of a single adult lactating female, exhibiting pouncing behaviour we attributed to hunting small mammals. We observed four out of five instances of hunting behaviour in tussock habitat.

Discussion

This study represents the second study of spring Wolverine diet north of the Brooks Range in Alaska (following Magoun 1987) and the first in the Colville River watershed. We documented a high prevalence of ungulates and cricetids in Wolverine scats, indicating the importance of these resources during spring. We also detected various predators (e.g., foxes), mid-size prey (Snowshoe Hare), and bird remains, documenting that Wolverines use a variety of prey types on the North Slope. Although we detected American Beaver in our scats, we attribute this to bait used by local trappers in the area as they are not a common species north of the Brooks Range of Alaska, although their range is increasing (MacDonald and Cook 2009; Tape *et al.* 2018).

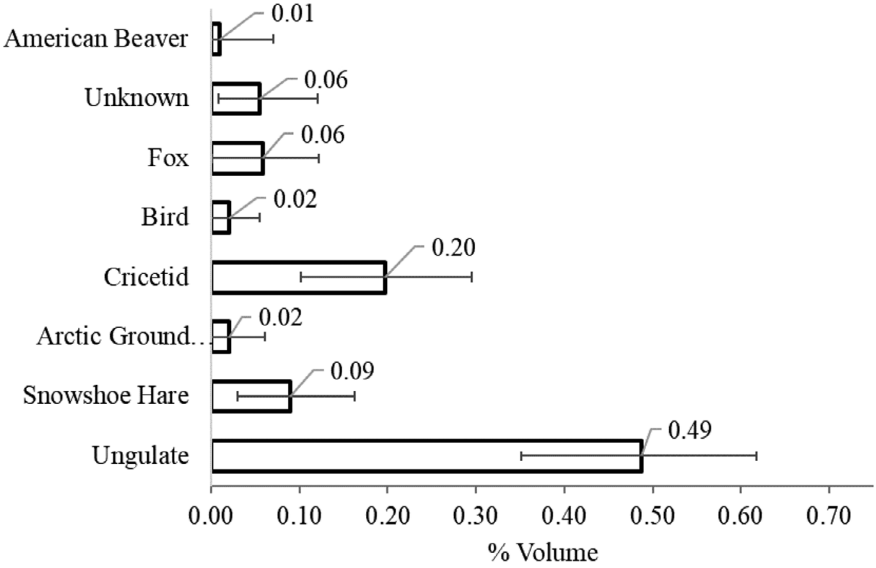

FIGURE 4. Volume and 95% CI for each of eight prey categories detected in Wolverine (*Gulo gulo*) scats collected while tracking and from GPS clusters near Umiat, Alaska, USA,10 March–29 April, and 29 May 2016. We weighed the samples then conducted an ocular estimate of the percentage of each prey item in the scat to determine percent volume. We estimated CI from 1000 bootstrap re-samplings. Prey detected includes: ungulate (Moose, [*Alces americanus*], Caribou [*Rangifer tarandus*]), Snowshoe Hare (*Lepus americanus*), Arctic Ground Squirrel (*Urocitellus parryii*), cricetids (Brown Lemming [*Lemmus trimucronatus*], Peary Land Collared Lemming [*Dicrostonyx groenlandicus*], Singing Vole [*Microtus miurus*]), bird (Aves), fox (Red Fox [*Vulpes vulpes*], Arctic Fox [*Vulpes lagopus*]), Ermine (*Mustela ermine*), American Beaver (*Castor canadensis*). Other (7%, including vegetation and woody debris) not shown.

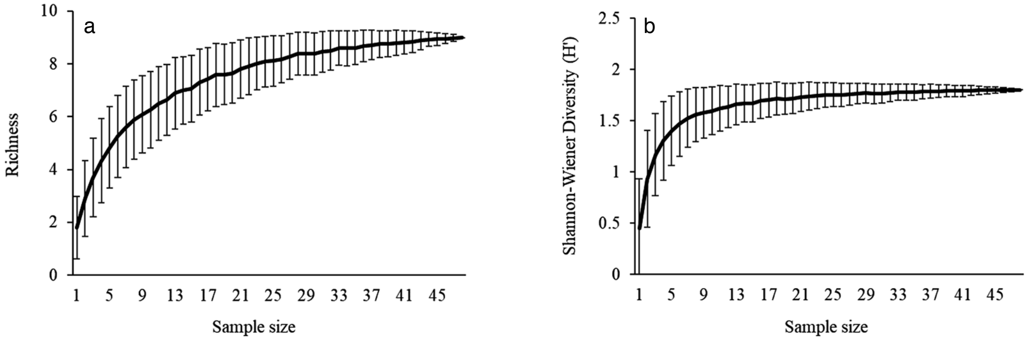

FIGURE 5. Rarefaction curves exhibiting the influence of sample size (x-axis) on Wolverine (*Gulo gulo*) diet richness (a) and diversity (b) estimated for scats collected near Umiat, Alaska, USA, 10 March–29 April, and 29 May 2016. Error bars show one SD estimated from 1000 bootstrap re-samplings of data.

Ungulates made up the largest portion of the Wolverines' diet based on our scat frequency and percentage of occurrence, and volume, which is similar to previous studies in North America and Fennoscandia (Lofroth *et al.* 2007; Dalerum *et al.* 2009; Koskela *et al.* 2013; Inman and Packila 2015). Moose contributed to diets of Wolverines in our study area, however due to their low abundance they likely are not a reliable prey source. The only Moose carcass we found provided an abundance of food for local Wolverines, but Caribou provide more overall biomass when available. Another Wolverine diet study in the southwestern Brooks Range (Dalerum *et al.* 2009), also found that Wolverines mainly subsisted on Caribou throughout the winter, despite the Western Arctic Caribou Herd's only seasonal availability (Lenart 2015). Dalerum *et al.* (2009) found that Caribou made up >50% of stomach and colon contents in Wolverine carcasses. Because winter Caribou distribution on the North Slope is inconsistent between years (Dau 2015; Lenart 2015), access to Caribou in the winter can be supplemented from food caches. We were unable to determine whether prey remains were from caching their own prey, scavenging other predator kills (such as from Gray Wolf [*Canis lupus*]), or from actively hunting. Obtaining this information would help reveal how Wolverines in our study area manage seasonally abundant ungulates compared to other prey sources (e.g., Arctic Ground Squirrel) that are less accessible in late winter. Similar to other studies basing diet inference on scats, only hair, bone, and feathers are available to determine FO and PO. This may underestimate a large prey item where large amounts of muscle are digested yielding a potentially smaller proportion of hair to biomass consumed. Other items, such as bird eggs may not be identified, but are known to be eaten by Wolverines (Magoun 1987; Samelius *et al.* 2002).

Although ungulates represent a significant portion of the Wolverines' diet in our and other studies (e.g., Mulders 2001; Dalerum *et al.* 2005, 2009; Lofroth *et al.* 2007; Inman and Packila 2015), cricetids are clearly another important prey. Cricetids composed the second highest frequency and percentage of occurrence, and volume for overall diet in our study. We also observed behaviour in spring consistent with hunting small prey, highlighting their potential significance as a spring food resource. Cricetid populations are irruptive and fluctuate over various temporal and spatial scales influencing their availability to Wolverines (Krebs and Myers 1974). The high proportion of cricetids detected in our Wolverine scats may reflect an abundance of cricetids throughout the study area. Wolverine scats could also contain a large proportion of cricetids because Wolverines preferentially selected them (Manly *et al.* 2002). Wolverines could increase their use of cricetids when snow begins to melt in the spring exposing subnivean prey at a time when the tundra tussock habitat is flooding with meltwater (as observed for the animals we saw hunting). However, without a measure of small mammal and ungulate abundance, it is unclear if Wolverines select for these prey resources on the North Slope, or adjust their intake based on availability alone during spring.

Cricetids, Snowshoe Hare, and Arctic Ground Squirrel collectively constitute 30% volume of spring Wolverine diet in our study. However, the role of small prey in Wolverine population dynamics is poorly understood and could be significant given the timing of availability relative to reproduction (Inman *et al.* 2012). Small mammal abundance in our area contributes to the diets of reproducing female Wolverines, when ungulates are only seasonally available, or as cached carrion. The availability and use of ungulates versus small mammals could influence Wolverine survival and reproductive success (Krebs *et al.* 2004; Persson 2005; Koskela 2013; Petersen 2014). Access to prey is particularly important when females are under increased energetic stress in late winter through summer while nursing and provisioning young with prey (Inman *et al.* 2012; Koskela 2013).

Future studies would benefit from determining diet composition of individual Wolverines to compare diet among home ranges. For example, a Wolverine that has an established territory in a riparian area may exclude another individual from access to a Moose carcass, thereby forcing the individual to find other prey sources. Our satellite collared Wolverines (R.D. unpubl. data), along with other radio tracking studies (Dawson *et al.* 2010; Persson *et al.* 2010), showed that Wolverines exhibit intrasexual territoriality, which likely precludes individuals of the same sex from accessing resources in neighbouring territories. Differences in diet among individual Wolverine territories could provide useful information on small-scale controls of population dynamics among habitat types, sex and age classes, and seasons.

Our work in the spring does not allow us to make inferences about summer diet. However, cricetids and Arctic Ground Squirrel may both be easier to hunt in summer months due to lack of snow cover and could be an important resource for Wolverine kits. In southern Norway, an abundance of cricetids in summer increased Wolverine kit survival (Landa *et al.* 1997). In addition, Arctic Ground Squirrel was an important diet resource for Wolverines on the western portion of the North Slope (Magoun 1987). Future studies would benefit from documenting summer Wolverine diets for kits and adults across a broader area, to determine the reliance on cricetids and Arctic Ground Squirrel, and their relation to Wolverine population dynamics.

Arctic Ground Squirrel represented only a small portion of the spring Wolverine diet in our study area, which differs from Magoun's (1987) findings, but may be confounded with the timing of our sampling. Near the Utukok River in the western portion of the North Slope, Wolverines fed on Caribou in mid-winter (December–February), but primarily fed on Arctic Ground Squirrel the rest of the year (Magoun 1987). Scats collected at the same time also contained large quantities of soil, likely from Wolverines digging up cached or hibernating Arctic Ground Squirrels (Magoun 1987). We observed negligible soil in the scats we sampled. However, the low frequency and percentage of occurrence and volume of Arctic Ground Squirrel in our analysis compared to Magoun (1987) could also relate to a difference in Arctic Ground Squirrel abundance and emergence dates between study areas. Our study area contains well drained soils preferred by Arctic Ground Squirrels, but their abundance is unknown (Barker and Derocher 2010). Assessing Arctic Ground Squirrel abundance and emergence throughout the area could aid interpretation of differences in the reliance on ground squirrels according to their activity and availability. This may be particularly important given the progressively earlier spring melt and potentially earlier availability of ground squirrels and cricetids through reduced snow pack (IPCC 2013). Furthermore, ground squirrels may increase in density in some well-drained areas as permafrost thaws in these northern ecosystems (Wheeler and Hik 2013).

To our knowledge, no other studies have used the Shannon-Wiener diversity index to calculate Wolverine diet diversity. We have no basis for comparing heterogeneity in resource use on the North Slope to other areas but monitoring how diet diversity changes over time or compares between areas could indicate differences in foraging strategies over time or among Wolverine populations. Future studies might consider adding this metric to their analysis to quantify how differences in resource use vary with the number of prey types in the diet. According to our rarefaction analysis, our sample size for diet richness may have been inadequate to provide accurate estimates of the average number of resources used by Wolverines. Future diet studies on the North Slope should consider increasing sample size to determine the full range of resources used by Wolverines.

A quantitative assessment of use versus availability would also provide improved insights into factors driving Wolverine prey selection, such as increased cricetid abundance, decreased ungulate abundance, or by the snowpack conditions affecting how cricetids and Arctic Ground Squirrels are accessible as the snowpack melts. Increased food availability corresponded with increased reproductive success of female Wolverines in Sweden (Persson 2005), thus, changes in food availability that influences reproductive success is a mechanism that could ultimately influence Wolverine abundance.

Author Contributions

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

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Use of stabilized thaw slumps by Arctic birds and mammals: evidence from Herschel Island, Yukon

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Abstract

As evidenced by animal sign (scat, active nests, nesting materials, rodent runways) observed across five stabilized retrogressive thaw slumps and two areas of undisturbed upland tundra, Arctic birds and mammals on Herschel Island, Canada, use stabilized thaw slumps differently than undisturbed tundra. Rodent winter nests and scat were found exclusively in undisturbed tundra and at a 250-year-old stabilized thaw slump site, whereas rodent runways and Semipalmated Plover (*Charadrius semipalmatus*) nests were found exclusively at 10- and 20-year-old stabilized thaw slump sites. Bird scat was found in each tundra type, but was most common in the youngest sites, and the number of observations decreased with increasing site age. Caribou (*Rangifer tarandus granti*) scat was found at all sites, whereas Muskox (*Ovibos moschatus*) scat was not found at 20-year-old sites and was most common in undisturbed tundra. To our knowledge, these observations are the first examples of birds and mammals using stabilized thaw slump habitat of different ages, and they provide new avenues of research for Arctic wildlife biologists concerned with the adaptation of these animals to permafrost disturbance and the resulting changes in vegetation cover.

Key words: Arctic; wildlife; thaw slump; Herschel Island; disturbance

Introduction

Retrogressive thaw slumps are among the most widespread thermokarst forms in the western Arctic, and each slump changes the physical and biotic characteristics of hectares of land (Mackay 1963; Cray and Pollard 2015). On Herschel Island, Yukon, Canada (69°36'N, 139°04'W, an area of 108 km^2), there are over 100 active thaw slumps, and, since the 1950s, thaw slumps in the western Arctic have been increasing in both area and number (Lantuit and Pollard 2008; Lantz and Kokelj 2008). Permafrost disturbances and related changes in flora may affect the spatial extent of fauna disproportionately by creating habitat heterogeneity that may alter how animals use the landscape (Forbes *et al.* 2001). By creating numerous large, discrete disturbances with distinct vegetation communities caused by the different age classes of the stabilized slumps (Cray and Pollard 2015), retrogressive thaw slumping and the associated stages of revegetation alter the tundra landscape; as the incidence and extent of these slumps increase, it becomes increasingly important to assess the potential consequences for wildlife.

Study Area

Part of the Yukon Coastal Plain, Herschel Island's mosaic of terrestrial, wetland, and littoral habitats is visited by diverse populations of migrating and nesting waterfowl, passerines, shorebirds, and raptors, as well as Porcupine Caribou (*Rangifer tarandus granti*) and Muskox (*Ovibos moschatus*). Of the 121 bird species recorded on Herschel Island, 46 use it as a breeding site (Yukon Bird Club 2015). The island is especially important as breeding habitat, as numerous Arctic-breeding species, particularly shorebirds, are in dramatic population decline (Gratto-Trevor *et al.* 2011). The four common small mammals recorded there are Northern Collared Lemming (*Dicrostonyx groenlandicus*), Brown Lemming (*Lemmus trimucronatus*), Tundra Vole (*Microtus oeconomus*), and Arctic Ground Squirrel (*Spermophilus parryii*; Krebs *et al.* 2011, 2012). These species are a fundamental part of the Arctic food web, as they are a food source for various avian and mammalian predators (Krebs *et al.* 2012). Small portions of the Porcupine Caribou herd spend time on Herschel Island, particularly from late April through August, with herds ranging in size from 21 to 75 individuals including bulls, cows, calves, and yearlings; in some years, Caribou have also been observed calving on the island (Cooley *et al.* 2012).

Methods

We recorded animal sign (scat, nests, rodent runways) in July 2011 from a total of 579 1 m × 1 m quadrats (Table 1) used in a vegetation community development study on slump stabilization (see Cray and Pollard 2015). Study sites on Herschel Island (Figure 1) included two stable upland tundra areas and five stabilized retrogressive thaw slumps representing three age classes: 10 years (two sites), 20 years (two sites), and 250 years (one site) since stabilization. For the 10- and 20-year-old stabilized thaw slumps, the year of stabilization was established by identifying the season in which there was

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Table 1. Animal signs, by type, observed in 579 quadrats in undisturbed tundra and various age classes of stabilized thaw slumps on Herschel Island, Yukon, Canada, July 2011.

Animal sign type	Undisturbed, no. (%)		250-year-old stabilized, no. (%)	20-year-old stabilized, no. (%)		10-year-old stabilized, no. (%)	
	U1 (*n* = 72)	U2 (*n* = 72)	E (*n* = 244)	A (*n* = 44)	D (*n* = 23)	B (*n* = 100)	C (*n* = 24)
Rodent nest material	7 (9.7)	5 (6.9)	5 (2.0)	0	0	0	0
Rodent runways	0	0	0	24 (54.5)	11 (47.8)	7 (7.0)	2 (8.3)
Rodent scat	0	1 (1.4)	4 (1.6)	0	0	0	0
Eider nest	0	0	1 (0.4)	0	0	0	0
Semipalmated Plover nest	0	0	0	2 (4.5)	2 (8.7)	0	0
Bird scat	2 (2.8)	0	7 (2.9)	7 (15.9)	3 (13.0)	19 (19.0)	13 (54.2)
Caribou scat	5 (6.9)	3 (4.2)	12 (4.9)	2 (4.5)	4 (17.4)	8 (8.0)	4 (16.7)
Muskox scat	3 (4.2)	1 (1.4)	1 (0.4)	0	0	1 (1.0)	0

no further headwall exposure or melt; the 250-year-old stabilized site was dated through sedimentological, geochemical, and accelerator mass spectrometry radiocarbon dating analyses by Lantuit *et al.* (2012).

Any recognizable scat was recorded; therefore, our observations likely consider droppings from multiple years. The number of quadrats sampled for each study site was scaled to 1% of the total area of each stabilized retrogressive thaw slump; 80% of these quadrats were spaced evenly along a transect perpendicular to the stabilized headwall, and the remaining 20% were distributed randomly within the stabilized area (for additional details see Cray and Pollard 2015). To maintain sampling uniformity, undisturbed areas were sampled with both transects and random quadrats in the same way as the other sites, where the median number of sample quadrats and the mean transect length were used for both undisturbed areas and the boundaries were assigned as a rectangle surrounding the transect (Figure 1).

Results

Rodent scat was observed only in the 250-year-old and undisturbed sites, whereas Caribou scat was observed in small amounts at every site (Table 1). Muskox scat was observed most frequently in the undisturbed sites and was not observed in the 20-year-old stabilized sites. Piles of dried grass and sedge material from rodent winter nests, 15–20 cm in diameter, likely representing complete nests (Krebs *et al.* 2012), were recorded at both the undisturbed and 250-year-old sites, although they were more frequent in undisturbed tundra. Nesting materials at the 250-year-old site were most frequently located near the headwall of the stabilized thaw slump. Surface grass tunnels, often referred to as runways (Krebs *et al.* 2012), were observed at the four 10- and 20-year-old stabilized slumps and were most common in the 20-year-old stabilized thaw slumps.

Although bird droppings were observed at every age class of tundra in this study, they were most frequent at the 10-year-old sites and decreased as site age increased. Of the five active bird nests we recorded, one was a Common Eider (*Somateria mollissima*) in the centre of the 250-year-old site and four were Semipalmated Plover (*Charadrius semipalmatus*) located in the approximate centre of the 20-year-old slump floors.

During the active period of a thaw slump and in the first few years following stabilization, animal tracks are readily observable in the soft mud of the slump floor (H.A.C. pers. obs.). Although not particularly useful for comparison between slump age classes, Muskox, Sandhill Crane (*Grus canadensis*), and Caribou tracks were also common in the slump floors of both 10- and 20-year-old sites.

Discussion

Based on our observations of animal signs, tundra birds and mammals appear to use stabilized slump surfaces and undisturbed tundra differently. Although our observations are limited to a small area and only one

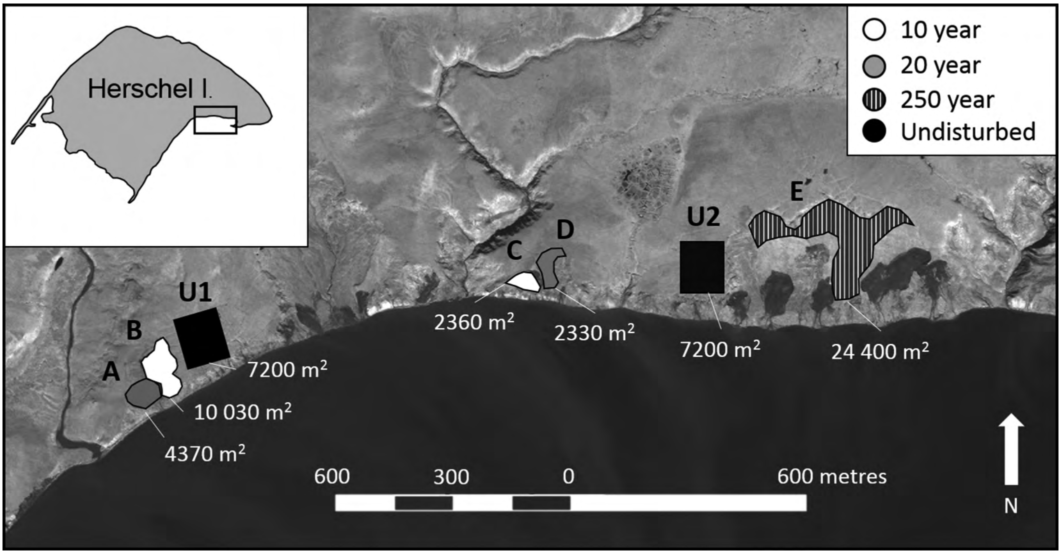

FIGURE 1. Locations of the seven study sites on Herschel Island, Yukon, Canada, including areas and age class of stabilized thaw slumps.

field season, these differences in rodent and bird habitat choice may be of interest to wildlife biologists for future study.

The occurrence of rodent burrows and winter nests near the headwall of the 250-year-old site could be because of the residual concave and steep morphology of long-stabilized thaw slumps, which leads to greater snow accumulation and, thus, thermal insulation for lemmings (Reid and Krebs 1996; Lantz *et al.* 2009; le Roux *et al.* 2011; Reid *et al.* 2011). As no rodent winter nesting materials were observed at the stabilized thaw slump sites, we suspect that the deposited dry, flat microtopography of the 10- and 20-year-old slumps is not preferred as winter nest sites. As all stabilized sites studied and many of the other more than 100 active and stabilized thaw slumps on Herschel Island are located in smooth or sloping uplands previously characterized by Arctic Willow/*Dryas*-vetch or cottongrass/moss vegetation type (Smith *et al.* 1989; Lantuit and Pollard 2008; Lantz and Kokelj 2008; Cray 2010, 2012), which is good year-round lemming habitat (Ale *et al.* 2011), the lack of burrows, rodent scat, or old nesting material at the 10- and 20-year-old sites suggests that an increase in the number and density of new thaw slumps may negatively impact rodent nesting habitat in the short term. However, rodent runways through the tall grasses were observed at all of the 10- and 20-year-old sites. In each area where there was a large percentage cover and height of grasses (i.e., 50% or more of the plant cover was >15 cm high), rodent runways were observed (Figure 2). Although no burrows or winter nests were found, rodents are likely making regular use of the 10- and 20-year-old sites as evidenced by the consistently trampled runways. Specific uses likely vary by species and may include foraging for graminoids and seeds and collecting nesting material.

On Herschel Island, Collared Lemmings have been shown to select dry habitat dominated by Entire-leaved Mountain Avens (*Dryas integrifolia* Vahl; Ale *et al.* 2011) and to have a diet of mainly willow (*Salix* spp. L.), *D. integrifolia*, and Mountain Cranberry (*Vaccinium vitis-idaea* L.; Batzii and Jung 1980; Rodgers and Lewis 1986). Although *D. integrifolia* is most prevalent in the undisturbed tundra sites (present at 92% of sites, average cover 9%), it is also present at the 250-year-old site (present at 43% of sites, average cover 3%; Cray 2012), and various species of *Salix* are common at all sites studied (Cray 2012), particularly Arctic Willow (*Salix arctica* Pallas), which is highly preferred by Collared Lemmings (Rodgers and Lewis 1986).

Brown Lemmings may also benefit from foraging in the vegetation community that establishes following thaw slump stabilization. Although Brown Lemming has a pronounced preference for wet meadow habitat, compared with Tundra Vole and Collared Lemming, it is a habitat generalist (Batzli and Lesieutre 1995; Ale *et al.* 2011) whose diet is dominated by monocots, particularly sedges such as Water Sedge (*Carex aquatilis* Wahlenberg) and cottongrass (*Eriophorum* spp. L.) as well as mosses (Batzli and Jung 1980). Although too dry to support *C. aquatilis* and too recently disturbed to have established *Eriophorum*, the stabilized thaw slump sites do support both higher frequencies and a higher percentage cover of mosses than undisturbed tundra (Cray 2012), and the graminoid-rich communities of 10- and 20-year-old sites likely provide suitable forage for Brown Lemmings.

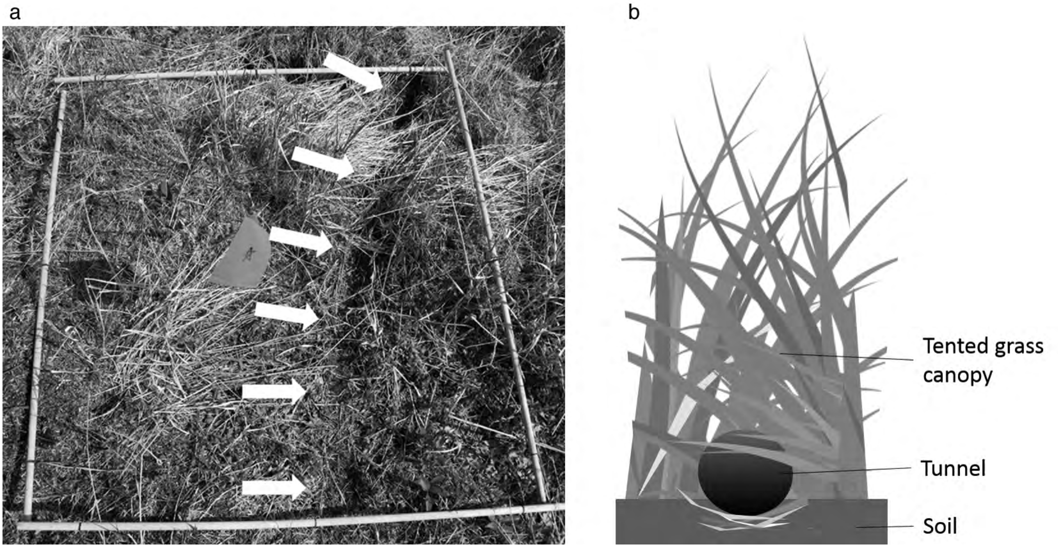

FIGURE 2. a. Photo of a quadrat in the 20-year-old stabilized thaw slump age class showing rodent surface grass tunnelling (runways). b. Lateral view of rodent runways through grass; note the tented canopy of grass obscuring the overhead view and the slight depression into the soil surface from repeated use. Photo and illustration: Heather Cray.

In contrast, although Tundra Voles have been shown to have a flexible diet including a variety of grasses, sedges, and forbs (e.g., lousewort [*Pedicularis* L.]) typical of the stabilized thaw slumps (Batzli and Jung 1980; Cray and Pollard 2015), this species is rarely found outside Pauline Cove, 3 km away from the study sites (Krebs *et al.* 2012); on Herschel Island, it has been shown to prefer very wet habitat dominated by *Eriophorum* spp., *Carex* spp., and *Salix* spp. (Ale *et al.* 2011), more characteristic of undisturbed tundra. Therefore, it is unlikely that Tundra Voles are responsible for the animal sign found in stabilized slumps.

Tundra bird species also use stabilized thaw slump floors, certainly as nesting sites which were directly observed, and possibly as foraging areas as well. As the quadrat method we used is not ideal for observing bird nests and observations were made during only one field season, our nest observations likely underrepresent the true use of these stabilized surfaces by bird species. Also, as we did not identify bird scat to species, it is difficult to determine potential preferences of specific birds for certain cover types or vegetation communities. Because distinct vegetation communities were found to be associated with each age of stabilized thaw slump in the study by Cray and Pollard (2015), forage opportunities (arthropods, seeds) and nesting habitat would be expected to differ as well.

For Semipalmated Plover, which prefer to nest in an open area with little to no plant growth, disturbed patches may actually increase their breeding habitat, which otherwise mainly consists of beaches or open pebbled areas (Nguyen *et al.* 2003). Indeed, the Semipalmated Plover is among the few plovers whose numbers increased between 1974 and 2009 and are currently stable (Andres *et al.* 2012), perhaps owing to its versatility in food choice or habitat expansion in the low Arctic as a result of disturbance (Nol and Blanken 2014).

Caribou scat was observed at every study site, suggesting that Caribou are at least travelling over if not grazing in every slump age class. Although the resilience of Caribou to vegetation change is contentious (Gunn and Skogland 1997; Callaghan *et al.* 1998; IPCC 2007), productivity of Caribou populations is strongly related to the quality and abundance of forage (Lenart *et al.* 2002) and the Porcupine Caribou Herd is known to forage extensively in the Tussock Grass (*Eriophorum vaginatum* L.) meadow community (cottongrass/moss) in the pre-calving and calving periods when *Eriophorum* heads are some of the first fresh vegetation available with significant biomass, cell solubles, nitrogen, and phosphorus (Russell *et al.* 1993). Although the cottongrass/moss vegetation type is generally considered stable (Smith *et al.* 1989), four of the five stabilized sites studied were located in this vegetation community, where thaw slumping initiated by coastal erosion progressed inland. Because *Eriophorum* does not recolonize stabilized thaw slumps even after 250 years (Cray and Pollard 2015), the significant increase in permafrost degradation expected with further climate change (Maxwell 1997) may affect the local availability of this vegetation type on Herschel Island and other upland areas prone to thaw slump activity, particularly areas adjacent to coastlines, lakes, and rivers.

Reductions in upland vegetation communities may also affect Muskox. The diet of Muskox consists mainly of graminoids, particularly sedges (e.g., *Carex* spp. and

Eriophorum spp.) and willows (*Salix* spp.; Ihl and Klein 2001; Larter and Nagy 2004), which are characteristic of undisturbed tundra sites on Herschel Island. Although stabilized thaw slumps are colonized by graminoid species within a few decades, the relative paucity of sedge and willow species at these sites (Cray and Pollard 2015) may explain the scarcity of Muskox scat observed at stabilized thaw slumps. With respect to winter forage, the increased snow accumulation within thaw slumps may also limit the availability of this food source for overwintering herds (Ihl and Klein 2001; Gustine *et al.* 2011).

Although our study indicates that mammals and birds appear to use recently stabilized thaw slumps, further investigation would be required to account for the complex biotic interactions and to predict consequences of the future, widespread permafrost disturbances expected with climate warming. As thaw slumps are expected to continue to increase in both area and number, the altered wildlife use associated with them present an interesting avenue for future research, particularly as the morphology, soil conditions, and vegetation community of stabilized slumps remain distinct from undisturbed tundra for over 250 years. To our knowledge, these observations are the first examples of birds and mammals using stabilized thaw slump habitat of different ages. We encourage all researchers working in these systems to record and report supplementary wildlife observations, as these observations play a useful role in building the larger wildlife and ecosystem knowledge base. Last, we suggest that long-term wildlife monitoring of stabilized thaw slumps would shed light on Arctic species' ability to adapt to permafrost disturbance and the resulting changes in vegetation cover.

Author Contributions

Writing – Original Draft: H.C.; Writing – Review & Editing: H.C. and W.P.; Conceptualization: H.C.; Investigation: H.C.; Methodology: H.C.; Formal Analysis: H.C.; Funding Acquisition: W.P. and H.C.

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Note

Clark's Nutcrackers (*Nucifraga columbiana*) caching Whitebark Pine (*Pinus albicaulis*) seeds in trees

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Abstract

On 17 September 2017, I observed two Clark's Nutcrackers (*Nucifraga columbiana*) from 8–10 m distance as they cached seeds in a stand of dead Whitebark Pines (*Pinus albicaulis*) at 2500 m elevation on Saint Mary Peak in the Bitterroot Mountains of Ravalli County, Montana. Over 5 minutes, the nutcrackers created 14 caches in seven different multi-trunk tree clusters in an area of about 50 m^2. All caches appeared to be single Whitebark Pine seeds, positioned 2–5 m (mostly 3–4 m) above ground in dead trees. Of the 14 caches, three were placed under loose pieces of bark on a trunk (one) or large limb (two), and the remaining 11 were in encrustations of American Wolf Lichen (*Letharia columbiana*) growing on branches of the dead trees. Nutcrackers are known to sometimes cache seeds above ground in trees during the late summer and autumn harvest of pine seeds, but usually not to the exclusion of other microsites. The ground at the Montana site was covered by 7–9 cm of fresh snow that fell the previous day, which may have encouraged the nutcrackers to place all of their seed caches above ground in trees.

Key words: American Wolf Lichen; caching behaviour; Clark's Nutcracker; *Letharia columbiana*; Montana; *Nucifraga columbiana*; *Pinus albicaulis*; tree caches; Whitebark Pine

Clark's Nutcracker (*Nucifraga columbiana*) is a major disperser of the large wingless seeds of Whitebark Pine (*Pinus albicaulis* Engelmann), the only *Cembrae* pine of five globally that occurs in the mountains of western North America (Tomback and Linhart 1990). During late summer and fall, nutcrackers harvest Whitebark Pine seeds from the indehiscent cones and transport as many as 150 seeds in a single load up to 30 km from the source tree, where they are often cached in the ground for later retrieval and use as a high-energy food source during the following winter, spring, and summer (Tomback 1978, 1998, 2001; Lanner 1982, 1996; Dimmick 1993; Lorenz *et al.* 2011). Thousands of seeds are scatter-hoarded by individual nutcrackers each year, more than the nutcrackers need for survival and reproduction (Hutchins and Lanner 1982; Tomback 1982). Seeds are often cached in microsites where they have a good chance of germinating if they are not retrieved or predated (Tomback and Linhart 1990). Thus, through their caching activities the nutcrackers ensure the persistence of Whitebark Pine by planting the seeds across landscapes where the pines are most likely to persist or become established and eventually produce more seeds, which also results in the continued availability of a food resource generally relied on by nutcrackers throughout the year (Tomback 1978, 1982).

Clark's Nutcrackers typically cache Whitebark Pine seeds at bill-depth in the ground at the base of trees or rocks, in open terrain on slopes, under forest litter, in dense moss, and among tree roots, fallen logs, and annual plants (Tomback 1978, 1982; Hutchins and Lanner 1982; Dimmick 1993). Caching seeds above ground in trees is infrequently reported across the range of the nutcracker (Tomback 1978; Dimmick 1993), although above-ground caching may be a regular behaviour of individual nutcrackers in some locations (Lorenz *et al.* 2011). Here I report opportunistic observations made of a pair of Clark's Nutcrackers caching Whitebark Pine seeds in dead Whitebark Pines. I provide details on the context of the caching activity and speculate about conditions that may encourage the choice of an arboreal microsite for caching seeds.

On 17 September 2017, while hiking to the summit of Saint Mary Peak in the Bitterroot Mountains, Ravalli County, Montana, I encountered two Clark's Nutcrackers at about 2500 m elevation caching seeds near the trail. The site (46.50569°N, 114.23336°W) was a stand of mature dead Whitebark Pine on the south-facing slopes of the peak. During 1055–1100 Mountain Daylight Time, I watched the nutcrackers from about 8–10 m with a 10× binocular as they performed their caching activities. I concentrated my attention on the closest bird, as both appeared to be behaving similarly. I saw the focal bird cache seeds 14 times, although the actual number of caches created was possibly double that amount during the 5 min of my observations, assuming both birds cached at the same rate.

All of the caches were located 2–5 m (mostly 3–4 m) above ground in seven different dead Whitebark Pines within an area of about 50 m^2, and all appeared to involve a single Whitebark Pine seed, based on the large size of the wingless seeds disgorged from the nutcracker's sublingual pouch to the tip of the bill and movement of the birds to new microsites after placing a single visible seed in a cache. Each bird paused and visually examined three or four microsites before caching a seed; at microsites where seeds were cached, the birds first probed two to five times with their bills. Three of the 14 caches were placed under flakes of bark on a vertical trunk ($n = 1$) or large limb ($n = 2$) of a dead pine, and the other 11 were placed in encrustations of American Wolf Lichen (*Letharia columbiana* (Nutt.) J.W. Thomson) growing in patches on smaller branches of the dead trees (Figure 1). I did not see the nutcrackers cover any of the caches with extra bark or lichens. Although my sample of caches is small, the nutcrackers appeared at that time to prefer caching their seeds above ground (100% of 14 caches), rather than in the ground, and in lichens more so than other microsites on the trees (one-sample proportion test; Statistix® 8, Analytical Software, Tallhassee, Florida, USA: Z [corrected] = 1.87, $P = 0.061$). At no time during the encounter did I see either bird descend to the ground. My observations terminated when a third nutcracker flew downslope over the two caching birds and gave two or three "kraack" calls ("short-location calls"; see Tomback 1998), whereupon the two caching nutcrackers responded with "mew calls" and immediately flew away in the direction the third bird had travelled.

The amount of caching of Whitebark Pine seeds in trees by the Clark's Nutcrackers I observed is high relative to most other reports of larger samples of caches made by nutcrackers, although still a small fraction of the thousands of caches made each year. On the eastern slope of the Sierra Nevada Mountains in California, Tomback (1978, 1982) observed nutcrackers make 80 separate caches, only three (3.75%) of which were in trees (two-sample proportion test: Z [corrected] = 8.26, $P < 0.001$). Also in the Sierra Nevada, Dimmick (1993) observed the creation of 937 caches, of which only about 19 (2.0%) were placed above ground in erect Whitebark Pines or Lodgepole Pines (*Pinus contorta* Douglas ex Loudon; Z [corrected] = 19.15, $P < 0.001$). Of at least 157 nutcracker caches reported in northwestern Wyoming (Hutchins and Lanner 1982), none were placed in trees, which is the same pattern I observed for 95 nutcracker caches made elsewhere in Montana (Marks *et al.* 2016), all of which were buried in the ground at bill-depth.

Caching in the ground is also the typical pattern for the Eurasian Nutcracker (*Nucifraga caryocatactes*) in northern Japan when caching seeds of Japanese Stone Pine (*Pinus pumila* (Pall.) Regel; Saito 1983; Kajimoto *et al.* 1998; Hayashida 2003) and in northeastern China when caching seeds of Korean Stone Pine (*Pinus koraiensis* Siebold & Zucc.; Hutchins *et al.* 1996). Only ground caches were reported in the Japan studies, whereas tree caches accounted for 11 (8.4%) of 144

Figure 1. Typical American Wolf Lichen (*Letharia columbiana*) growth on a dead branch of Whitebark Pine (*Pinus albicaulis*) in which Clark's Nutcrackers (*Nucifraga columbiana*) cached pine seeds in the Bitterroot Mountains, Ravalli County, Montana. The lichen patch is about 30 cm in length. Photo: P. Hendricks.

caches reported in the China study (*Z* [corrected] = 8.66, $P < 0.001$).

In sharp contrast with the earlier studies, Clark's Nutcrackers on the eastern slopes of the Cascade Range in Washington state regularly cached pine seeds in trees (Lorenz *et al.* 2011), and tree caches of Whitebark Pine seeds in particular made up 129 (64.8%) of 199 caches made by radio-telemetered birds. This is still less than the proportion of tree caches in my sample (*Z* [corrected] = 2.41, $P = 0.016$), but indicates that caching pine seeds in trees may be routine under some circumstances by some nutcracker populations. It is worth noting, however, that only 11 (5.5%) of the caches of Whitebark Pine seeds reported by Lorenz *et al.* (2011), both in trees and in the ground, were made in Whitebark Pine forest, unlike in Montana where all 14 caches I observed were in this forest type. Furthermore, most tree caches in the Cascades study, regardless of forest type, were in live trees among needle clusters, in lichen clumps within the foliage, and under pieces of bark. The microsites for the caches I noted in Montana fit in the last two categories, but all caches were in dead trees lacking any foliage other than arboreal lichens, unlike in Washington. Also, the lichens in which the Washington caches were placed were not identified or described, so it is unclear how similar or dissimilar the lichen cache microsites really are.

Lorenz *et al.* (2011) noted that nutcrackers caching seeds in live trees are less conspicuous than birds on the ground and may be overlooked unless they are telemetered, which could explain why they were observed more often caching Whitebark Pine and Ponderosa Pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) seeds in trees than in studies lacking a telemetry component (Tomback 1978; Hutchins and Lanner 1982). Lorenz *et al.* (2011) also suggested that the amount and duration of winter snowpack could influence the magnitude of ground caching, because snow cover inhibits future access to ground caches (Tomback 1978) but not caches in trees. Earlier studies reporting caching behaviour were conducted at the lower latitudes of California (Tomback 1978, 1982) and Wyoming (Hutchins and Lanner 1982) in drier forest types with less winter snowpack than the Cascades, possibly favouring a greater amount of ground caching at those locations.

The Montana nutcrackers I encountered were quite visible in the dead pines, which lacked any foliage other than lichens, and it was easy to observe them caching seeds. Nevertheless, limited data from Montana (Marks *et al.* 2016) indicate that ground caching by nutcrackers may be routine in Whitebark Pine forest during the harvest of pine seeds, as it is in California (Tomback 1978, 1982; Dimmick 1993) and Wyoming (Hutchins and Lanner 1982). Here, factors in addition to future cache accessibility during winter and spring may affect choice of cache microsites. In particular, access to an array of potential microsites at the time of cache creation could influence the incidence of caching pine seeds in trees. When I made my observations, the ground at the Montana site was covered with 7–9 cm of soft snow, which had fallen the previous day. The two nutcrackers I encountered showed no inclination to cache pine seeds in the ground, which could have been purely a response to the presence of an ephemeral snow cover that interfered with location of potential cache microsites on the ground rather than any general preference by the birds to cache seeds in trees. Frequent use of lichens as a microsite for tree caches may have been a result of lichen abundance in the absence of other foliage.

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Revisiting the hypothesis of sex-biased turtle road mortality

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Abstract

Road mortality poses a major threat to turtle populations. Several studies have suggested that the terrestrial movements associated with nesting increase this risk for females. The Ontario Turtle Conservation Centre (OTCC) is home to the Kawartha Turtle Trauma Centre, which admits 900 or more turtles a year, with road injuries the primary cause of admission. We tested the hypothesis that road mortality in turtles is female-biased using data from injured Midland Painted Turtles (*Chrysemys picta marginata*), Snapping Turtles (*Chelydra serpentina*), Blanding's Turtles (*Emydoidea blandingii*), and Northern Map Turtles (*Graptemys geographica*) collected over about 126 000 km^2 and admitted to OTCC's hospital from January 2013 to October 2017. There was no difference in the number of male and female admissions of Midland Painted, Blanding's, or Snapping Turtles ($P > 0.05$); however, more female Northern Map Turtles than males were admitted ($P < 0.001$). Admission of female turtles peaked in June during the nesting season, but male admissions were more evenly distributed throughout the season. Our admissions data provide a temporally unbiased and geographically broad snapshot of turtle–vehicle interactions that can directly inform conservation and management policies. Although our data are not equivalent to mortality rates, these results demonstrate that vehicle strikes can have a substantial impact on both female and male turtles.

Key words: Midland Painted Turtle; Snapping Turtle; Blanding's Turtle; Northern Map Turtle; *Chelydra serpentina*; *Chrysemys picta*; *Emydoidea blandingii*; *Graptemys geographica*; Ontario; road ecology; road mortality; sex-biased dispersal; sex ratio; wildlife rehabilitation

Introduction

Roads have been called the "sleeping giant" of conservation biology (Forman and Alexander 1998) because of their pervasive negative impact on biodiversity and habitat connectivity. The effects of roads include habitat fragmentation, barriers to movement, genetic isolation of population fragments, and direct mortality from vehicle–wildlife collisions (Strasbourg 2006; van der Ree *et al.* 2011; Beebee 2013). Smaller, slower wildlife species may be more susceptible to vehicle strikes because they take more time to cross a road, increasing the probability of interaction with a vehicle, and may not use flight as a predator response, further increasing the likelihood of vehicle strikes (Fahrig and Rytwinski 2009). Turtles are particularly vulnerable to mortality caused by vehicle strikes because their long lifespan and slow population growth rates magnify the population-level impact of small increases in adult mortality (Congdon *et al.* 1993; Gibbs and Steen 2005; Crawford *et al.* 2014; Rytwinski and Fahrig 2015).

Several studies have tested the hypothesis that female turtles are at higher risk of road mortality during the nesting season because overland movements required to find a suitable nest site may increase females' probability of contact with roads (Steen and Gibbs 2004; Aresco 2005; Gibbs and Steen 2005; Steen *et al.* 2006; Patrick and Gibbs 2010; Dorland *et al.* 2014). In addition, females that nest on the shoulder of paved roads, even those that have repeatedly nested at the same area, can spend considerable amounts of time searching the road, whereas males typically cross the road and do not show this nest-searching behaviour (R. Brooks pers. comm. 11 May 2018). If road mortality is female-biased, then the adult sex ratios of turtle populations should gradually become male-biased (Steen and Gibbs 2004; Gibbs and Steen 2005; Steen *et al.* 2006; Patrick and Gibbs 2010; Dupuis-Désormeaux *et al.* 2017).

Road mortality studies often do not report the sex of the turtles (e.g., Ashley and Robinson 1996; Gunson *et al.* 2014; Baxter-Gilbert *et al.* 2015; Coquette and Valliant 2016; Dupuis-Désormeaux *et al.* 2017) or only report the sex of a limited sample (Haxton 2000). In addition, some road mortality surveys are carried out for a limited portion of the active season (e.g., Haxton 2000) or for a limited number of days throughout the season (e.g., Cureton and Deaton 2012). A temporally unbiased dataset of road mortality occurrences in male and female turtles is required to test directly the hypothesis of sex-biased road mortality occurrences in turtles at the landscape scale.

The Ontario Turtle Conservation Centre (OTCC; https://ontarioturtle.ca/) is home to Canada's only dedicated turtle rehabilitation centre. The OTCC admits turtles injured in a variety of ways, but the vast majority of admissions (80–95%, depending on the species) represent turtles injured on roads across southern Ontario. Southern Ontario contains 92% of Ontario's human population and some of the highest concentrations of roads on the planet with a road located, on average, every 1.5 km (Gunson 2010; Laurance *et al.* 2014). Admissions to the OTCC include all eight species of turtles native to Ontario, including the globally endangered Spotted Turtle (*Clemmys guttata*; van Dijk 2011) and Blanding's Turtle (*Emydoidea blandingii*; van Dijk and Rhodin 2011). All Ontario species except Spiny Softshell (*Apalone spinifera*) have been admitted with vehicle-related injuries.

Admissions to the OTCC have increased steadily since 2010 (Figure 1), in part because of increased public participation following intensive public education initiatives. The OTCC admissions dataset provides an opportunity to test the hypothesis of sex-biased road effects on a large, temporally unbiased and geographically broad sample of turtles struck by vehicles across an area of approximately 126 000 km^2. We used OTCC data to test the hypothesis that interactions with vehicles affect more female turtles than males, predicting that if more females than males are struck by vehicles in our intake area, then counts of turtles admitted to the OTCC would also be significantly female biased.

Methods

Located in Peterborough, Ontario (44.336776°N, 78.348319°W), the OTCC is the home of the Kawartha Turtle Trauma Centre (KTTC), which receives cases from across southern Ontario and occasionally from southern Quebec. Turtles are brought to the OTCC by members of the public and field biologists or transferred from other wildlife rehabilitation centres when complex veterinary care is required. Admissions include all species of turtles native to Ontario, but the majority are Midland Painted Turtles (*Chrysemys picta marginata*), Snapping Turtles (*Chelydra serpentina*), and Blanding's Turtles. During admission, OTCC staff record each turtle's species, sex, size (carapace length and width), and age class (hatchling, juvenile, or adult), as well as the reason for admission and the collection location. Admissions to the hospital take place all year round; however, most occur from mid-April to late October, during the active season of turtles in southern Ontario.

Vehicle strikes typically cause life-threatening injuries to turtles (Figure 2), and medical records from the centre confirm that successful outcomes and rehabilitation of turtles hit by vehicles depend on rapid veterinary treatment. Therefore, these turtles would have died in the absence of treatment, and their admissions data are an appropriate proxy for vehicle-related mortalities.

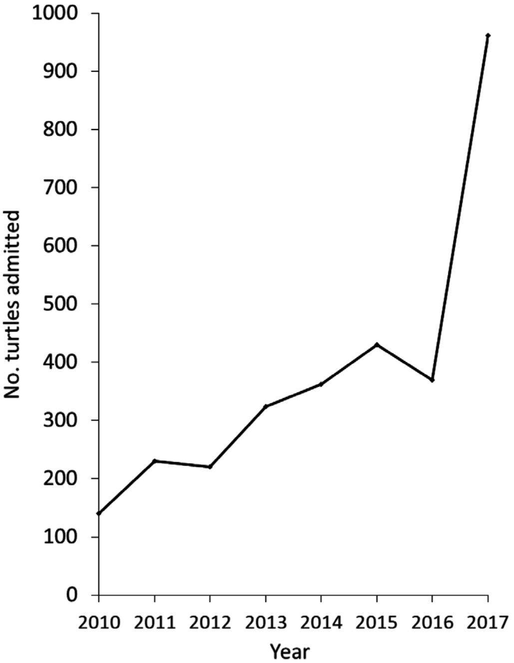

Figure 1. Increase in admissions to the turtle hospital at the Ontario Turtle Conservation Centre since 2010.

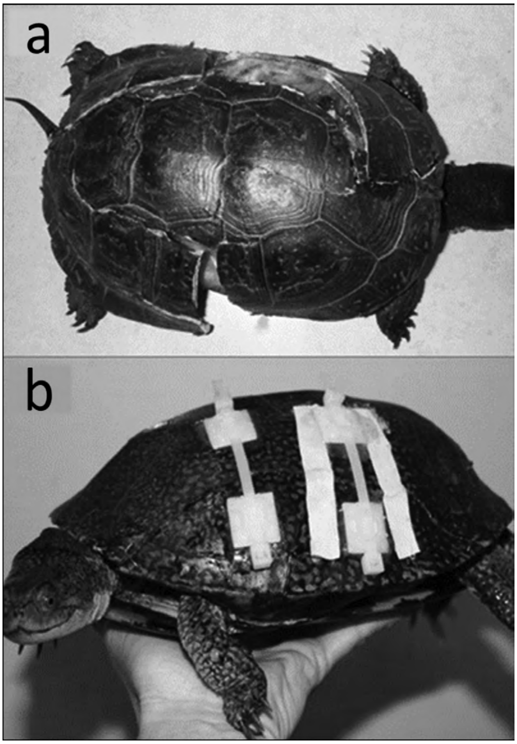

Figure 2. a. Injuries from vehicle strikes are typically life-threatening, as in this Blanding's Turtle (*Emydoidea blandingii*), but rapid surgical attention often allows turtles to recover. b. Blanding's Turtle that was successfully rehabilitated and released back into the wild. Photos: S. Carstairs.

Successfully rehabilitated turtles are released back into the wild near their initial collection location.

We used OTCC admissions data from January 2013 to October 2017 to test whether vehicle strikes on turtles occur more frequently in one sex than the other. We removed the records of turtles that were admitted for other reasons and limited our data set to those hit by a vehicle. We tested for significant deviations from an unbiased sex ratio in the admissions data by performing a nonparametric binomial two-sided test based on a one-sample binomial distribution (Wilson and Hardy 2002) with the untested assumption that the populations of turtles in the study area were also not sex biased. All statistics were performed in Microsoft Excel (Microsoft Corporation, Redmond, Washington, USA), and we considered results significant at $\alpha = 0.05$. Location data were mapped using ArcMap 10.1 (ESRI, Redlands, California, USA).

Results

During the study period, the OTCC admitted 2355 turtles, of which 2020 were admitted due to vehicle strikes (Figure 3). Of these, 1722 were mature individuals and were sexed during the admission process; Wood Turtle (*Glyptemys insculpta*) vehicle strikes are not shown due to locational sensitivity. Most vehicle strikes involved Midland Painted Turtles (62%), followed by Snapping Turtles (29%), and Blanding's Turtles (6.5%; Table 1). Approximately half (51%) of turtles admitted because of vehicle strikes were female, and admissions of female Midland Painted Turtles, Snapping Turtles, and Blanding's Turtles peaked in

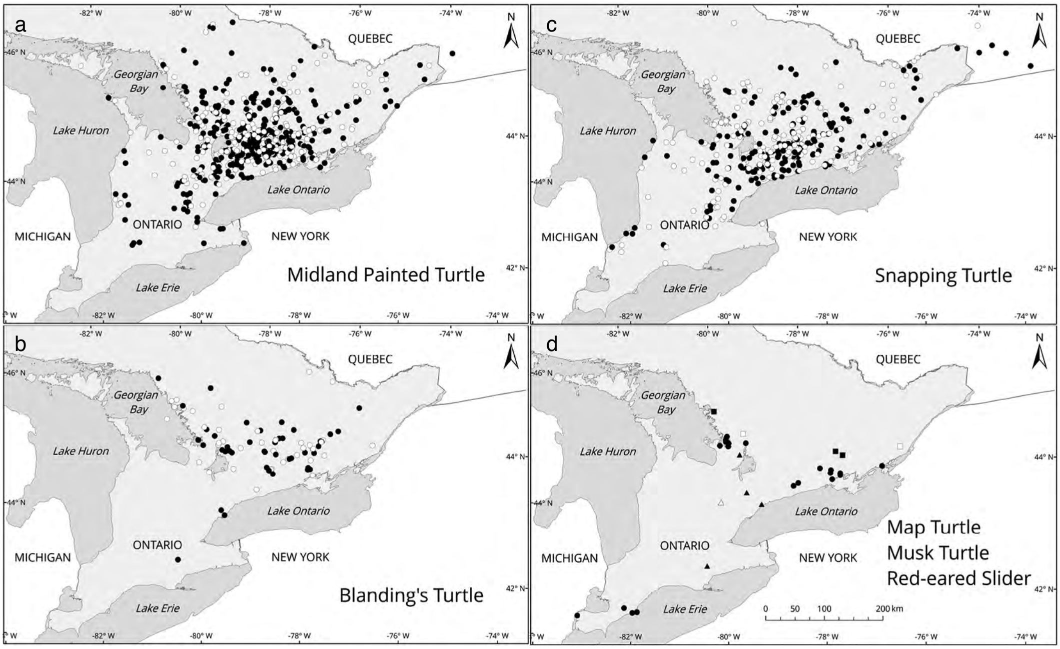

FIGURE 3. Locations of vehicle strikes of adult turtles admitted to the Ontario Turtle Conservation Centre, 2013–2017. Open symbols = males; black-filled symbols = females. In the lower right panel (d), circles indicate Northern Map Turtles (*Graptemys geographica*); squares indicate Eastern Musk Turtles (*Sternotherus odoratus*); and triangles indicate Red-eared Sliders (*Trachemys scripta elegans*).

TABLE 1. Species and sex distribution for 1722 adult turtles admitted to the Ontario Turtle Conservation Centre because of vehicular collisions from 2013 to 2017.

Species	Females	Males	Proportion of males	*P**
Painted Turtle (*Chrysemys picta*)	541	532	0.496	0.404
Snapping Turtle (*Chelydra serpentina*)	249	254	0.505	0.606
Blanding's Turtle (*Emydoidea blandingii*)	63	49	0.438	0.120
Northern Map Turtle (*Graptemys geographica*)	32	2	0.059	<0.001[†]
Total	885	837	0.486	0.129

*Indicates cumulative probability that the observed sex ratio reflects an unbiased binomial distribution centred around 0.5.
[†]Sample was significantly biased toward one sex or the other ($\alpha = 0.05$).

June, concurrent with the nesting season for these species. Admissions of male turtles showed multiple clusters extending from early spring to late fall (Figure 4). Turtles were admitted for care following vehicle strikes as early as 13 March (2013), as late as 25 October (2017).

A binomial test showed that admissions of male and female turtles struck by vehicles, when combined over all five years, were not statistically different for Midland Painted Turtles ($P = 0.404$), Snapping Turtles ($P = 0.660$), or Blanding's Turtles ($P = 0.110$; Table 1). Admissions of Northern Map Turtles (*Graptemys geographica)* were significantly female biased ($P < 0.001$), but map turtles made up only 2% of all vehicle-related admissions.

Discussion

Our temporally unbiased, 5-year admissions dataset from the OTCC does not support the hypothesis of sex-biased road mortality in Midland Painted, Snapping, or Blanding's Turtles, but suggests that roads may have a greater impact on female Northern Map Turtles than on males. The OTCC admits turtles year round, enabling continuous collection of road mortality data over five years and accurate sexing of each turtle admitted. Our road mortality data are count data, like those of most other road ecology studies, and cannot be converted to mortality rates because robust demographic data are available for only a few well-studied turtle populations. However, the even distribution of road mortality occurrences among males and females of the most commonly hit species in our dataset suggests that the impact of roads on turtles is more evenly shared between the two sexes than previous studies have suggested.

Painted, Snapping, and Blanding's turtles frequently move over land to find mates, to access resources such as foraging or overwintering sites, or to find a suitable nest site (Pettit *et al.* 1995; Tuberville *et al.* 1996; Ernst and Lovich 2009). These activities bring both males and females of these three species into contact with roads, as reflected in our data. Nesting season is clearly associated with increased risk of road injury for female turtles in Ontario. However, our results also provide empirical support to a recent modelling approach (Beaudry

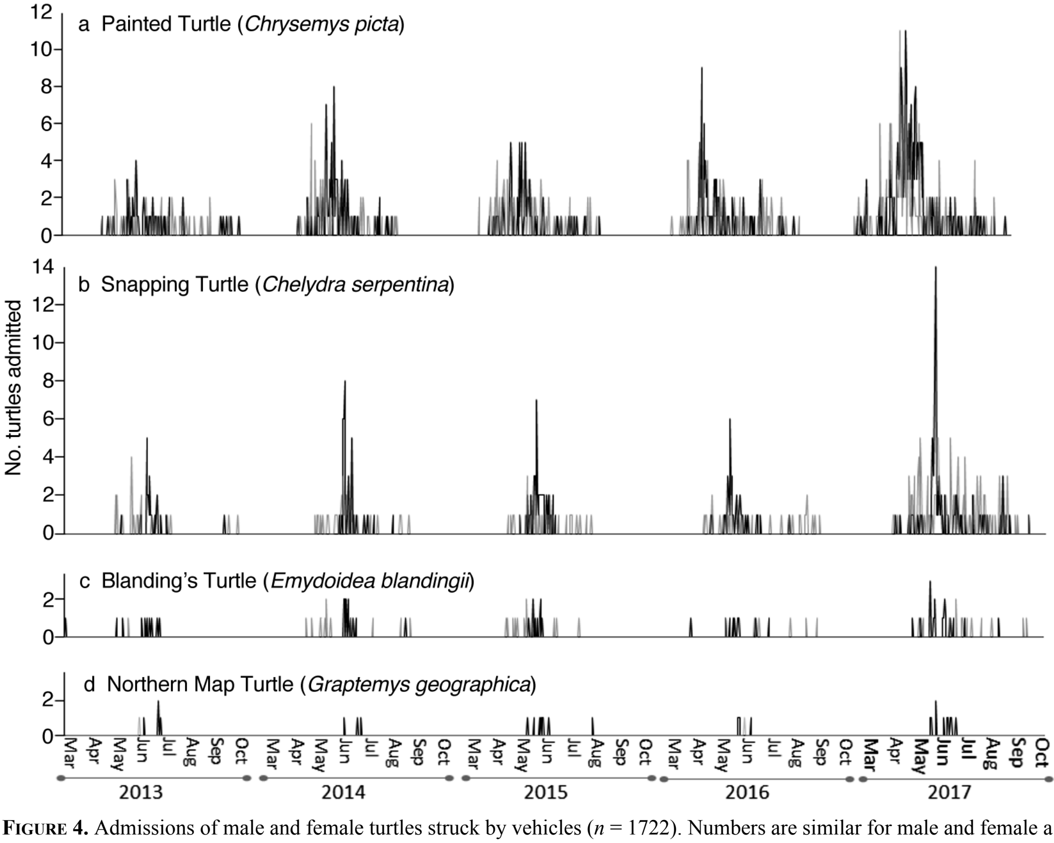

Figure 4. Admissions of male and female turtles struck by vehicles ($n = 1722$). Numbers are similar for male and female a. Midland Painted (*Chrysemys picta*), b. Snapping (*Chelydra serpentina*), and c. Blanding's Turtles (*Emydoidea blandingii*). Admissions of female turtles (black lines) peaked during the nesting season, while admissions of males (grey lines) were more evenly spread through the season. d. Northern Map Turtle (*Graptemys geographica*) females were more likely to be admitted than males. No admissions caused by vehicle strikes occurred from November to February.

et al. 2010) that suggests that male mortality is similar to female mortality when the entire active season of mid-April to the end of October is considered. Beaudry *et al.* (2010) found that male and female Blanding's Turtles had similarly long movement patterns and were both similarly exposed to road mortality. However, males moved more than females, before and after nesting season.

Although our sample of Northern Map Turtles was small (n = 34), it was heavily biased toward females (94%). The behaviour of Northern Map Turtles is consistent with this observation: male Northern Map Turtles are almost exclusively aquatic, whereas females emerge rarely, usually only to find a suitable nest site (Ernst and Lovich 2009).

Survivorship in female turtles has been a focus of turtle ecologists and conservation biologists for good reason; it has an extremely high impact on the growth rates of turtle populations (Congdon *et al.* 1993; Heppell *et al.* 1996; Heppell 1998; Mitrus 2005; Enneson and Litzgus 2008). Therefore, maximizing female survivorship is considered a key component of effective turtle conservation. Nevertheless, reproductive males and females are required to sustain a viable turtle population, and conservation programs should ensure adequate survival rates in both sexes. Most methods used to mitigate road impacts on turtles (ecopassages, drift fencing, etc.) probably provide equal protection to both sexes. Road closures during the nesting season may adequately protect nesting female turtles but fail to protect males and females moving overland during the rest of the active season.

One tool used to recover threatened turtle populations is "headstarting", in which eggs are hatched in artificial conditions that maximize success and eliminate nest depredation. Hatchlings are often also reared for some amount of time before release, which may reduce the risk of early juvenile mortality (e.g., Iverson 1990; Haskell 1996; Bennett *et al.* 2017). In species with temperature-dependent sex determination, incubation conditions can be controlled to produce a predetermined sex ratio in hatchlings. Setting aside the many factors that can prevent recruitment of headstarted or wild-hatched juveniles to a turtle population, our data add evidence to suggest that headstarting projects or other attempts to augment populations should consider both sexes and not focus solely on females. The fact that females spend more time on roads, and yet males are struck in equal numbers, also illustrates the high impact of roads on the male population.

Converting mortality count data, such as those presented here, to mortality rates for male and female turtles in a population and, thus, inferring and projecting population level impacts requires knowledge of the sex ratio of the underlying population—a major limitation of our study and of many others. Accurately estimating population sex ratios requires substantial survey effort, and some survey methods do not have equal detection rates for both sexes. For example, hoop traps may capture male-biased samples of Painted Turtle populations (Ream and Ream 1966), while surveys of turtle nesting sites are necessarily female-biased. Furthermore, counts of road mortality for long-lived animals, such as turtles, do not accurately represent demographic trends (Rytwinski and Fahrig 2015), and unequal male and female road mortality rates could cause yearly fluctuations in the population's sex ratio as the population nears extinction.

The underlying reasons for the discrepancy between the equal sex ratio in road injuries that we found and the increasing male-biased population sex ratios correlated with higher road densities found in numerous other studies (e.g., Marchand and Litvaitis 2004; Steen and Gibbs 2004; Aresco 2005; Gibbs and Steen 2005; Steen *et al.* 2006; Patrick and Gibbs 2010) remain uncertain. We urge road ecologists to remain critical of the underlying assumptions in the interpretation of mortality counts, and we urge turtle researchers to be cautious of assumptions that could inadvertently prioritize protection of one sex over the other.

The morbidity and mortality of reptiles admitted to wildlife care facilities in North America has been described previously (Hartup 1996; Brown and Sleeman 2002; Rivas *et al.* 2014), but these studies focus on the veterinary medicine aspects of rehabilitation. Our study demonstrates how admission data from a wildlife rehabilitation centre can be used to address broader questions in conservation and draw inferences about threats to wild populations. Perhaps a future approach to these and new data would be to examine the sex ratio variation with location and to compare traffic, road density, or population composition. There are numerous possibilities, but our large sample at a landscape level is unique and could be explored further. Turtles are long-lived and slow to mature and the survival rate of eggs and hatchlings is low. Turtle populations cannot recover quickly from increased adult mortality (Brooks *et al.* 1991). Conversely, offsetting increased mortality can have a relatively large impact on demographic rates, such that rehabilitation and release of injured turtles may have a population-level effect.

Acknowledgements

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Book Reviews

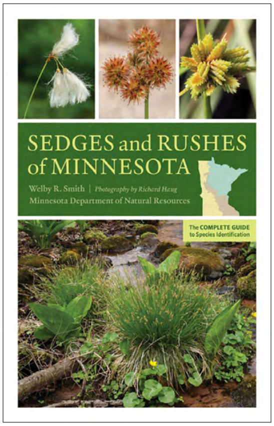
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those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

Currency Codes: CAD Canadian Dollars, USD US Dollars, EUR Euros, AUD Australian Dollars, GBP British Pound.

BOTANY

Sedges and Rushes of Minnesota: The Complete Guide to Species Identification

By Welby R. Smith. Photography by Richard Haug. 2018. University of Minnesota Press. 696 pages, 1100 colour plates, and 248 maps, 39.95 USD, Paper.



Over the past decade or so, several states or regions in North America (e.g., Maine, New England, Pacific Northwest, Wisconsin) have had guides published on the identification of the sedges (Cyperaceae) found within their boundaries. This guide to the sedges and rushes (Juncaceae) of Minnesota is one of the most recent additions to this list, and reflects the increasing interest among field botanists in understanding and being able to identify members of this large, diverse, and ecologically important group of graminoids. The inclusion of the rush family in the Minnesota guide is a welcome addition that the other guides mentioned above do not cover.

The book begins with basic information on sedges and rushes, and explains that the main purpose of the book is to provide a tool for field botanists who want or need to identify these plants within their study areas. Thus, the book is aimed at anyone who might be conducting biological inventories, whether professional or amateur. The author has made a concerted effort to use non-technical terms whenever possible and, when not possible, has provided simple explanations of the technical terms. The introductory sections of the book also include acknowledgements of those who assisted with production, including the primary photographer, Richard Haug, who has done a great job of representing the important features of each species with his images. These sections also contain some basic information, including maps, on the ecology of the state as it relates to plant distributions (major substrate types, historical vegetation types, and vegetation zones).

The main contents of this book are the sedge and rush identification aids, including keys, photographs, descriptions, and range maps. The first key enables identification of the genera of sedges and rushes in Minnesota. From there, all of the genera are arranged alphabetically, and within genera (and within sections in the large genus *Carex*) species are also arranged alphabetically. This can mean that similar-looking species within related sections in the genus *Carex* may not be situated close to each other within the book, but that should not be a major impediment for most users. The species concepts used in the book reflect the most current thinking regarding the taxonomy of these plants, in a few cases being even more current than that found in *The Flora of North America* treatments for these families (Brooks and Clemants 2000; Ball *et al.* 2002).

The treatment of each genus begins with a description based on the species found in Minnesota, along with basic information on the diversity of the genus worldwide, in North America, and in the state. Accompanying photographs focus on the most important and characteristic features of the genus that will aid in identification. Next comes a key to the species in the state, followed by species accounts. Each species has two pages dedicated to it: the first is a full page of descriptions, notes on how to differentiate the species from similar ones, and habitat notes, along with a distribution map; the facing page contains images of important identification features and characteristic habitat. The descriptions, notes, and images are all well done, focussing on the important features required for identification of the species.

In the case of the genus *Carex*, however, which is by far the largest genus covered in the book, additional text is devoted to describing the unique features and architecture of the inflorescence, again accompanied by excellent annotated photographs. This is followed by a key to the sections within the genus, and then each section is covered alphabetically in the same way that genera are treated elsewhere in the book. Each section contains a key to the species, along with representative photographs, and then the species are treated in alphabetical order within the section.

This is an excellent guide to the sedges and rushes of Minnesota, and will be applicable to much of the Midwest and adjacent portions of Manitoba and western Ontario. The keys are workable, the descriptions are good and easily understood because of the plain language explanations that are provided where the author deemed that they were needed, and the photographs are excellent. If one considers that the book is written with Minnesota in mind, rather than the globe, then the content is accurate and thorough. (However, if one were to look at the Cyperaceae with a global view, then there are other genera with perigynia, not just *Carex*; p. 14.) In a few cases, additional characters could have been included to make recognition of a species even easier (e.g., the glaucous nature of the foliage in *Carex canescens*, the gynecandrous terminal spike of *C. gracillima* relative to the staminate terminal spike of *C. arctata*, glossy appearance of the perigynia in *C. pallescens*), but the keys, descriptions, and photographs should virtually always lead the user to the correct identity. I do have a few minor quibbles, such as slight discrepancies in colour descriptions, particularly of the achenes, where the photographs sometimes illustrate colours not reflected in the descriptions (due to degree of maturation of the achenes); however, these will rarely if ever affect the usefulness of the book. There are very few typographical or grammatical errors, and my sense is that the book has been produced with a great amount of care and attention to detail.

There is only one aspect of the organization of the book that bothers me: the lack of separation between the two families in the main body of the text. There are only two genera of Juncaceae in the flora (*Juncus*, *Luzula*), and the flower structure of the family is so different from that of Cyperaceae. Therefore, it would have been a simple matter to separate, rather than intersperse, the two families, without losing anything in the process. Rather, in my opinion, something would have been gained, in terms of the user's understanding of the differences between the two families.

Overall, this book provides an excellent, user-friendly guide to the sedges and rushes of Minnesota. I recommend it highly to all field biologists involved in botanical inventories in the central part of the continent, and to students of these two families in general.

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Ball, P.W., A.A. Reznicek, and D.F. Murray. 2002. Cyperaceae. Pages 3–608 *in* Flora of North America North of Mexico, Volume 23. *Edited by* Flora of North America Editorial Committee. Oxford University Press, New York, New York, USA.

Brooks, R.E., and S.E. Clemants. 2000. Juncaceae. Pages 211–267 *in* Flora of North America North of Mexico, Volume 22. *Edited by* Flora of North America Editorial Committee. Oxford University Press, New York, New York, USA.

WILLIAM J. CRINS

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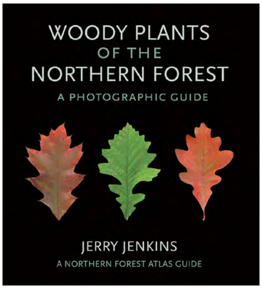
Woody Plants of the Northern Forest – A Photographic Guide

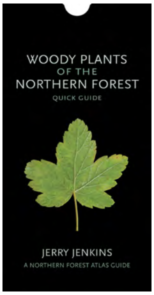
By Jerry Jenkins. 2018. Comstock Publishing Associates – An Imprint of Cornell University Press. 64 pages, 25.50 USD, Paper.

Woody Plants of the Northern Forest – Quick Guide

By Jerry Jenkins. 2018. Comstock Publishing Associates – An Imprint of Cornell University Press. Foldout Chart, 11.95 USD, Paper.



The Northern Forest Atlas (NFA) and its principle director, Jerry Jenkins, have produced a beautiful, easy-to-use, and innovative identification book, the *Woody Plants of the Northern Forest – A Photographic Guide*. The accompanying *Quick Guide* and online material help to fulfill the aims of the NFA in producing ground-breaking resources, targetted at naturalists and ecologists, to aid in fostering conservation and stewardship of the Northern Forest Region. Lying between the oak forests of the eastern United States and the boreal forests of eastern Canada, the Northern Forest Region is one of the largest, most diverse, and contiguous of temperate forests and, as the author stresses, is of utmost ecological importance. With a focus on rapid identification, based on multi-image composite photos, these resources provide an accessible, modern approach to field guides.



The *Photographic Guide* (its 10 × 11" size is ideal for backpack or coffee table, but not pocket) is intended to help rapidly identify twigs and leaves of woody plants through a series of quick photographic keys and more systematic sections. Nineteen 'quick guides' (not to be confused with the *Quick Guide* folding charts) at the front of the book help separate groups with distinctive features, for example thorns or lobed leaves. Not all of the 235 species photographed possess distinctive features and therefore not all appear in one of the quick guides. The rest of the book is divided into systematic sections arranged to rapidly arrive at species identification. These systematic sections divide the species into five groups: evergreens, opposite buds, alternate buds, opposite leaves, and alternate leaves. Species within each group are arranged alphabetically by family and genus.

The *Photographic Guide* is very user-friendly: its content is divided in a straightforward and accessible manner that lends itself to rapid orientation, in contrast to the frequently overwhelming nature of many woody plant identification guides. Similar species are easily comparable, with brief annotations to help guide towards identification suggestions; in fact, the author stresses that the guide serves to "suggest and eliminate, but not confirm" (p. 1). It is also noted in the introduction that not every woody plant encountered can be identified by leaves or twigs alone, with some groups requiring bark and sometimes flowers. This brings me to one of my only criticisms of the *Photographic Guide*: why not include photographs of bark or flowers for these trickier groups? In truth, this information is available via the Northern Forest Atlas website (http://northernforestatlas.org/), but I don't see why it could not be included here, unless the aim of basing these guides solely on leaves and twigs overrides the need to confirm a positive species identification for all specimens. There is definitely merit in stimulating the questioning process and to encourage utilizing a range of available resources.

The photographs themselves are integral to this modern field guide approach—with each studio photo taken from multi-image composites. Stacking technology and software produce a single image by combining the sharpest points from each of a series of frames. This results in beautifully fine detailed images, rich in depth and with even the finest twig bud details appearing crystal-clear. This technique also results in variation and imperfections in many of the specimens, with the author describing some to be "meaningful" and some "accidental" (p. 1)—the user is cautioned in the introduction that this variation mirrors what will be encountered in the field. The author goes on to assign the user the task of determining where "casual variation ends and species lines begin" (p. 1), implying the importance of individual exploration and continued learning. A visual glossary at the front of the *Guide*, and a gallery of photos of full tree photos at the end, round out this resource nicely. Although the gallery could easily have been expanded to include shrubs, it does a succinct job of identifying the tree species for which a profile or silhouette is a useful and viable approach to identification.

The companion *Quick Guide* folding charts provide a more pocket-friendly version of the *Photographic Guide*. The package comprises two charts, "winter" and "summer", each printed on durable, water-resistant paper. The winter chart focusses on the twigs and buds, whilst the summer chart concentrates on identification mostly from leaves, although much of the "evergreen" sections are duplicated. This results in highly practical field tools that are tailored to specific field seasons, and therefore aid in speeding up the identification process through making these resources as efficient as possible for the active field naturalist.

The affordable price tag for the *Quick Guide* and the *Photographic Guide* make either a welcome addition to any naturalist's library. The unique arrangement of the *Photographic Guide* and the versatility of the *Quick Guide* result in each having its functional role, and helps advocate for those who wish to invest in both resources. Online users are able to access a library of high-resolution images ranging from aerial to near microscopic photos, in addition to downloadable charts and other products. A forthcoming digital atlas and new guides to sedges of the Northern Forest are signs of more ground-breaking work in the pipeline. The reaffirmation from Jerry Jenkins across all of these physical and digital resources is that the purpose of the Northern Forest Atlas Project is to document the beauty and diversity of these vast forests, whilst providing tools for the next generation of conservationists looking to study and protect them. These two offerings on the *Woody Plants of the Northern Forest* certainly do an innovative job in meeting these goals.

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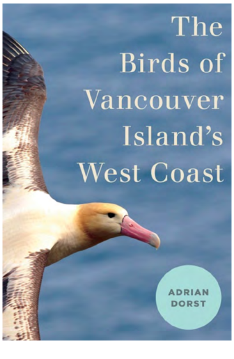
ORNITHOLOGY

The Birds of Vancouver Island's West Coast

By Adrian Dorst. 2018. UBC Press, On Point Press. 544 pages and 140 black and white photographs/maps, 39.95 CAD, Cloth.



Adrian Dorst's new book on the birds of the wild west coast of Vancouver Island is an engagingly-written, straightforward, and thorough account of the region's avifauna. The author has lived in Tofino for over four decades and has spent all those years "recording the comings and goings of birds" (p. 13) in his wilderness neighbourhood. He knows the region intimately—the rich pelagic waters, the wave-scoured rocks, the long beaches that stretch off into the mist, the quiet inlets, the great forests, and the rugged, almost inaccessible mountains. He also loves this area, and this love comes through on every page.

This is not a field guide, but rather a detailed account of the occurrence and ecology of each of the 360 bird species known from the region. In addition to his extensive personal experience, the author has gathered information from a wide variety of sources, including birding websites, the scientific literature (355 references are cited at the back of the book), the four volumes of *The Birds of British Columbia* (Royal BC Museum and UBC Press, 1997–2001), and an earlier account of the region's birds that he co-authored, the *Birds of Pacific Rim National Park* (BC Provincial Museum, 1978). The acknowledgments run to three and a half pages! Black-and-white photographs are scattered through the book—Adrian Dorst is well-known as a photographer, so these illustrations are all high-quality.

Following a brief but informative introduction dealing with the climate, topography, and ecology of the west coast, the story of each species is told in individual accounts of up to four pages. Each species account begins with a short, one- or two-paragraph introduction describing the bird and its global and provincial range, and then proceeds to detail regional habitat use, migration timing and other changes through the year, and trends over the decades.

The accounts are clearly and cleanly written in narrative form and although the subject is scientific, the prose is not technical. This is a book that one can pick up and pick a page at random and enjoy learning about a particular bird during a brief read. A flavour of the style can be seen in sentences like the one describing a recent increase in Hairy Woodpecker records, particularly those by a certain young birder—"Keep in mind that most of us do not have the benefit of Ian's acute hearing" (p. 339). (I have also gone birding with the young man in question and can attest to the acuity of his hearing and accuracy of his identifications!)

Although this is a style that I enjoy, another aspect of the accounts can make the biological story a little harder to follow than it needs to be. What is absent are graphs that could summarize changes through the year, or changes over the decades (for example, a graph of records through the year could quickly show a migration pattern). This may be simply a personal preference but, for readers like me, it would be easier to see those stories visually, rather than read detailed sentences about numbers.

Although the book is focussed on the west coast of Vancouver Island, the author makes sure that the reader knows the big picture story of the region's birds. For example, he tells the story of the Short-tailed Albatross's near-extinction on its Japanese nesting islands, and mentions threats facing shearwaters on their distant breeding grounds. We learn that the Japanese tsunami of 2011 killed an astonishing 110 000 Laysan Albatross chicks and 2000 adults on Midway Atoll. A detailed account of Canada Goose numbers over time includes a discussion of the effect of the 1964 Alaska earthquake on the breeding geese that migrate through Tofino.

"Nature nuggets" are similarly sprinkled through the text. For example, we learn that Pacific and Winter Wrens diverged as long ago as 4.3 million years and, because Golden-crowned Sparrows love to nip off the tender leaves of garden vegetables, "[l]ong-time gardeners may therefore be more knowledgeable than field ornithologists as to just when the migration period begins and ends" (p. 454). I was surprised to read that Steller's Jays are absent year-round from the Broken Group in Barkley Sound, presumably because they are reluctant to cross an expanse of open water. Another surprise was an account of a small wintering population of Myrtle (Yellow-rumped) Warblers on Stubbs Island near Tofino, where they feed on the berries of "a profusion of wax-myrtle [Pacific bayberry] bushes" (p. 440).

Keen birders know that the west coast of Vancouver Island is a magnet for wandering birds that have gone astray. The book concludes with detailed accounts of the 50 accidental species recorded for the region, from Solander's Petrel (the first well-documented record for North America) and Falcated Duck (I remember the spur-of-the-moment drive from Victoria to 'tick' that one!) to an astonishing Prothonotary Warbler. A further 26 species are listed as "Hypothetical", because they lack photographic or other evidence.

For any naturalist visiting the west coast of British Columbia, this is a valuable reference and an enjoyable book to read. Happy birding!

Syd Cannings

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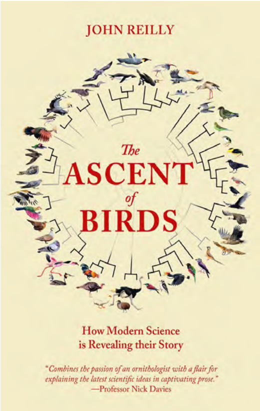
The Ascent of Birds: How Modern Science is Revealing Their Story

By John Reilly. 2018. Pelagic Publishing. 340 pages, 31.99 CAD, Cloth.



This book tells the fascinating story of the evolution of birds from their origins in Mesozoan Gondwanaland, which broke up between 130 and 50 million years ago, to their current worldwide distribution. I admit that when I first read the title, I thought this book would be about the dinosaur–bird transition and, while that is covered, it is a relatively minor story in the book. Reilly starts at the base of the avian phylogenetic tree, with the ratites, a diverse group of flightless birds that include ostriches and rheas, and proceeds chronologically towards the offshoots that gave rise to the finches and tanagers. Dr. Reilly is not a specialist in avian evolution (he had an illustrious career as a haematologist and blood cancer specialist) but combines his scientific training with a life-long interest in birds to present complex concepts and rapidly evolving research in a lively and accessible style.

The book is divided into two almost equal parts: non-passerines (13 chapters) and passerines (14 chapters). Each chapter is spearheaded by a named bird, from tinamous to tanagers, and begins with a look at the evolutionary history of the family or species of the chapter title, followed by discussion of some of the specialized anatomical, physiological, and behavioural adaptations for those species. An example would be Chapter 5, "The Penguin's Story: Phenotype and Environment". While Reilly's basic question is "how did penguins evolve to survive the extreme polar environment?", he begins the story some 70 million years ago, in the Upper Cretaceous, when penguins split from other seabirds and then dispersed throughout the Southern Hemisphere. He then discusses their adaptations: changes in feather density and structure that aid in insulation in extreme temperatures; heat "exchangers" in feet and flippers; operation of their flippers by muscles located deep within their warm body and manipulated by long tendons; solid rather than air-filled bones that help deal with dive pressures; haemoglobin modifications to carry more oxygen; and social adaptations such as taking turns shuffling to the outside of the circle when incubating eggs.

Some of Reilly's "disarmingly simple" questions, such as why are there so many (well over a thousand) South American sub-oscines (the supposedly more primitive members of the passerines that have less well-developed vocal organs than the oscines), turn out to be unexpectedly complex, combining the effects of geographical isolation, geological upheavals, climate change, vicariance, and many unusual ecological niches. Many chapters include phylograms (family trees drawn by comparing gene sequences from different species) to show evolutionary relationships of bird families, which is the basis for most of the author's stories. Phylograms are really just scientific hypotheses waiting for more data to confirm or refute them, or for new analytical techniques to be developed. Because Reilly's career is not invested in the research, he even-handedly discusses conflicting hypotheses and interpretation of data in a number of instances. The advent of molecular genetics has enabled taxonomic relationships to be revealed, resulting in many recent changes among taxa. For example, Hepatic (*Piranga hepatica*) and Scarlet (*P. olivacea*) tanagers have traditionally been classified within the Thraupidae (Tanagers), but they are now known to be cardinals, while honeycreepers, seedeaters, conebills, saltators, Darwin's finches, and flowerpiercers are really tanagers … a good excuse to get a new field guide every year!

The occasional simple map shows the movement of continents or the dispersal routes of species. The 37 colour plates in the middle of the book, comprised of 51 images, complement the text. There is a tremendous volume of supplementary material, including a timeline, a chart of geological ages, a comprehensive glossary, 32 pages of chapter notes and citations (in reduced type), bibliography, list of species (376) mentioned in the text (in a nice touch that section is titled "Dramatis Personae"), and an index. The bibliography is rather short (three pages) because most of Reilly's sources are primary papers, of which there are no end of interesting ones to follow up on in the notes section.

While this book is a little daunting at first, covering as it does the entire evolutionary history of birds, the author does an excellent job of breaking the latest science down into understandable chunks, and I highly recommend it as an excellent synthesis of this amazing field of research. You won't look at birds the same again.

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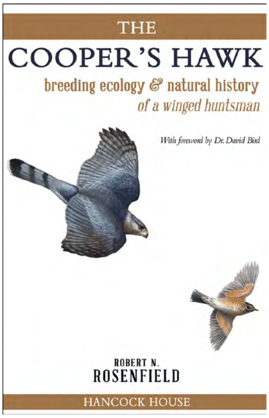
The Cooper's Hawk: Breeding Ecology & Natural History of a Winged Huntsman

By Robert N. Rosenfield. 2018. Hancock House. 164 pages, 49.95 CAD, Cloth, 34.95 CAD, Paper.



One could think of Cooper's Hawk (*Accipiter cooperii*) as a "feeder bird", because it frequently hunts mid-sized birds attracted to feeders, such as sparrows, starlings, and doves, and chipmunks that are attracted to spilled seed. They hunt mostly ground- and shrub-foraging birds and small mammals from a perch, scanning for movement, followed by a sudden burst of flight. They will even run after prey on the ground or dive into thick cover in pursuit. Having evolved as a forest raptor, with adaptations for swift flight through tight spaces, the species has adapted well to fragmented urban environments with abundant prey as long as there is nesting habitat.

In his Preface, Rosenfield sets out three goals for the book: 1) to aid the curious public in interpreting the behaviour of Cooper's Hawks and to recognize their ecological contexts, 2) to serve agency and academic biologists charged with management of raptors, and 3) to prompt new questions for study. The author tackles these goals in six chapters, broadly titled as: "You are What You Eat", "Courtship and Nesting Biology", "The Breeding Population and Habitat Suitability", "Individual Traits (the Descriptive Currencies of Natural History Dynamics)", and "The Meaning and Implication of Natural History Variation".

I think the author achieves these goals admirably. This book is a well-written account of the natural history of Cooper's Hawk, based on the author's own 38 years of research in Wisconsin and other studies in

British Columbia, North Dakota, Arizona, and Florida. It is a good example of how a long-term study of a single species (six generations) enables a researcher to explore questions they didn't even know to ask in the beginning. Rosenfield is an author on approximately one-quarter of the papers in the lengthy reference section, but he enlivens his research results with incidental observations to weave a compelling story. The text is supplemented with numerous photographs with extensive descriptive captions that are a significant addition to the information presented. There are a few maps and sketches.

The problem I have with the book is the layout. The 15 cm × 23 cm size is very nice, but to achieve that the publishers used very narrow margins, such that to read the text near the spine you must force the book flatter. Most photos 'bleed' right to the edge of the page, including the bound edge such that part of the photo is effectively hidden. Multiple photos are laid out side-by-side with no border or white space to separate them or give eye relief. Many photos appeared to be very grainy, perhaps the result of scanning original slides at insufficient resolution or cropping distant photos to emphasize the bird in the picture. And captions run very tightly to the edge of the photos. These layout choices were undoubtedly influenced by trying to keep the number of pages to 164—most book printing relies on 'signatures' in multiples of four for more economical printing. I doubt if any of these decisions were Rosenfield's.

While I found these layout issues distracting, I do recommend this book to anyone interested in Cooper's Hawks. As Rosenfield says in the final chapter, "… without comprehensive natural history accounts of where a species lives, how it behaves, and what it eats, a species is simply a dot on a graph" (p. 133).

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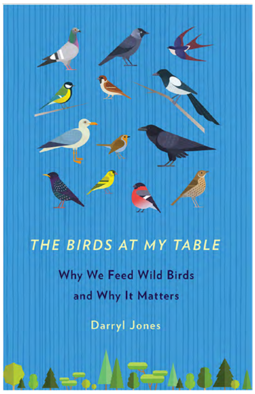
The Birds at My Table: Why We Feed Wild Birds and Why It Matters

By Darryl Jones. 2018. Cornwell University Press, Comstock Publishing Associates. 352 pages, 19.95 USD, Paper.



The central purpose of *The Birds at My Table* is aptly explained by the subtitle *Why We Feed Wild Birds and Why It Matters*. While it may at first seem unlikely that Canadian naturalists would be interested in a book on bird feeding written by a behavioural ecologist from Australia, the author delivers an exceptional overview of both the science and art of intentional bird feeding throughout the world. It is not at all a how-to book on feeding birds, but rather an exploration of the human, avian, and economic dimensions of what was once a simple backyard process engaged in by people around the world but is now a global industry. The author takes a common, almost universal human-wildlife interaction that many may never have thought about deeply, and highlights its major implications, both positive and negative, for wildlife ecology. The book explores many aspects of bird feeding that I never really contemplated, despite having fed birds for almost my entire lifetime. Many dimensions of bird feeding are delved into, from the early history of bird feeding and the huge growth in the bird feeding industry, the debate over whether to feed just in the winter or year-round, the effects of supplementary feeding on bird populations, human perspectives on and reasons for bird feeding, the role of bird feeding in disease transmission, the valuable role of citizen science in monitoring bird populations, and supplementary feeding as a species recovery and conservation measure.

The author makes it clear that he was not an expert on the science of feeding birds when he first initiated his research. He is refreshingly candid and open about what his expectations were and what findings surprised him, and engagingly and understandably conveys those lessons to the reader. The informative and eloquent style kept even the Acknowledgement section interesting and engrossing.

The history and diverse facets of bird feeding around the globe are informatively presented. To many, bird feeding is a common phenomenon of little ecological or social importance. But it is now virtually a global phenomenon, and it is easy to forget that the first mass marketing of wild bird seed and feeders only began in the 1960s. The scale of bird feeding is astonishing, and the author presents interesting and sometimes staggering statistics without resorting to dry facts. For example, in the United States alone 20 000 railway cars-full of black sunflower seed are sold annually, globally over one million tons of seed are sold annually worth $5–6 billion, in New Zealand over 5 million loaves of bread are fed to birds annually, fully one-half of the population in many countries feeds birds, and in the United Kingdom enough bird seed is sold annually to support many times the populations of birds being fed.

The book provides an interesting summary of the history and evolution of bird feeding, from the casual sharing of available food scraps with neighbourhood birds to the deliberate, year-round feeding of birds using manufactured feeding devices and food grown specifically for the bird feeding market. The metamorphosis of black sunflower seed in just a few decades from a native plant cultivated by indigenous peoples of North America and consumed naturally by relatively few bird species to the primary seed fed to and consumed by birds globally was a fascinating story. Interesting parallels are drawn between the growing environmental consciousness in the early 1900s, the conservation movement and the establishment of the first USA national parks, and a growing public interest in bird feeding that led to a rapidly expanding demand for wild bird feeding and feeding products.

A truly international picture of bird feeding today is presented. The anecdotes and references are taken from many countries, and the author interviewed experts from many countries in the course of his research. There are many Australian, New Zealand, and European references, and from a North American perspective it is interesting to learn about the similarities and differences of bird feeding habits and perspectives elsewhere in the world. It was enlightening to learn that bird conservation agencies around the world hold very different and sometimes completely contradictory perspectives on major questions, such as whether to feed birds only in winter, year-round, or not at all.

The book is thoroughly researched and solidly referenced, although there has been surprisingly little research until recent decades. While noting the limited availability of scientific information, he has compiled a diverse array of both current and historical resource materials from the scientific literature, bird food supply companies, bird conservation agencies, and others. The available scientific literature has been thoroughly gleaned and summarized. Without compromising the integrity of individual studies, Jones presents complex and complicated results in a way that the lay audience can understand. This is not easy, as many studies come to different or even contradictory conclusions. Without sparing readers from the challenges of inadequate research, differing techniques, differing species ecology, and inconsistent results, he familiarizes them with the challenges of scientific investigation and interpretation of results. He succinctly provides general conclusions and observations on bird feeding, while still recognizing the complexity and diversity of results, and notes when his conclusions or suppositions are hypothetical or based upon subjective evaluation. References are presented by both chronological footnotes by chapter as well as an alphabetical listing by author. Unfortunately, this method is clear but cumbersome and somewhat inefficient, requiring double the effort to find a reference; sometimes the same reference is cited several consecutive times, but there is no way to know this until the chapter summary is consulted.

Areas where scientific research and documentation are limited are clearly identified. The author saves his greatest incredulity for the lack of research, and his most overt indication of humour for the "virtually universal pastime of 'feeding the ducks down at the lake,' a practice that leads to untold tons of bread being tossed to waterfowl the world over" (p. xiii). But the humour is ironic, however, for Jones goes on to note the dual result: "bringing joy to millions and often resulting in the eutrophication of urban lakes and a host of attendant ecological problems" (p. xiii). He returns to this topic later in the book, so clearly he is very interested in, and perturbed by, the amount of bread fed to waterfowl and frustrated over the lack of research on the implications of this practice.

The book is well written and edited. It was a bit surprising that there was only one passing reference to the potential implications of extensive supplemental feeding for natural selection, given the dramatic effects on bird survival and populations; I assumed that this topic would have featured much more prominently. It was also surprising that, although there were references to many types of food and birds around the world, the supplementary feeding of nectar-feeding birds such as hummingbirds was not mentioned. There was one minor misrepresentation of biological fact that can be forgiven in a Southern Hemisphere author: Black-capped Chickadees are referenced as being at the northern limit of their range in Wisconsin, when in reality they occur almost as far north as the treeline.

Many unique and interesting aspects of avian ecology and conservation are mentioned throughout the text. This includes information on species such as the Monk Parakeet, an aggressive invasive in the eastern USA that is sustained in winter only through the use of feeders, Noisy Mynas in Australia that are attracted by the planting of native nectar-bearing shrubs and then exclude most other species through their aggressive territorial behaviour, and the role of supplementary feeding in the recovery of species at risk such as Red Kite (United Kingdom) and Takahe (New Zealand).

The chapter on disease transmission was a fascinating and sobering summary of the known and potential role of feeders in the dissemination of avian diseases, through both viral transmission where birds congregate and tainted foods such as peanuts with aflatoxins.

This book will be of interest to both naturalist and scientific audiences interested in the art and science of feeding birds. North American readers will get a refreshing and interesting global perspective on bird feeding. Readers will find that the answers to the basic question, *Why We Feed Wild Birds and Why It Matters*, are both simple and complex, and they will find much to ponder in this book. Those who feed birds will come away with a renewed understanding and awareness of the role of supplementary feeding in the ecology of birds, and will look at feeding birds in a new and broader way.

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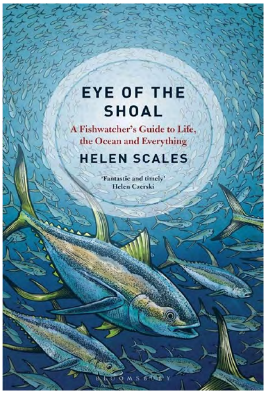
ZOOLOGY

Eye of the Shoal

By Helen Scales. 2018. Bloomsbury Sigma. 320 pages, 36.00 CAD, Cloth.



This book is an excellent example of a highly qualified professional researcher distilling the most interesting parts of her subject to create a coherent, enthralling work. Like her previous book, *Spirals in Time: The Secret Life and Curious Afterlife of Seashells* (Scales 2015), *Eye of the Shoal* is a 'deep dive' into the history, ecology, and complexity of life in the watery realm. Of the two, *Eye of the Shoal* is by far my favourite.

The 10 chapters cover the past and present representatives and ecologies of "fish", that nebulous group of (usually) water dwellers who (often) have scales and display an impressive diversity of colour, behaviours, diet, habitat, and talents. Although at least a passing interest in fish or aquatic ecosystems will probably help, this book is written for a broad audience and requires no specialized knowledge to enjoy. Latin names are only given if their translations are relevant or interesting, and the history of fish research is treated with humour and based in the quirky personalities of those who were involved in it.

The author is trained as a marine biologist and her field experience in marine ecosystems combines with a presenter's sense of organization to create an eminently readable book. Unlike some works in the genre, Scales lets the subject speak for itself. Yes, you may come away caring more about the health and preservation of earth's fishy residents, but it will be because the author showed you the wonders of that world, not simply because she told you to care.

The text is organized in sections, many one or two pages long, covering a specific topic. This structure makes for an excellent sporadic read (short reading over a cup of hot caffeinated liquid of your choice, or before bed), but there is a well-crafted, logical flow to each section and the text does not feel fragmented, disorganized, or repetitive.

Helen Scales writes with many excellent habits that are the hallmark of great general science writing, including humanizing science. Where appropriate and without the impression of haphazard name dropping, discoveries and studies are contextualized with the location and name of the researchers leading them. This allows interested readers to look up these projects and adds a face and context to facts and discoveries.

This book feels like a passion project in the best possible way and includes several delightful touches that put it a step above other entries in the genre. Each chapter begins with a full-page drawing by scientific illustrator Aaron John Gregory capturing the themes and main species of the chapter, each of which is annotated in the back material with a species list. Continuing the attention to detail, sections within a chapter are separated by a small fish, with each chapter having its own dedicated icon. A final touch: each chapter ends with a short traditional fish myth, its origin, and its own thematic illustration.

The author's easy to follow, narrative prose combined with her contagious enthusiasm make *Eye of the Shoal* one of the most enjoyable popular science books that I have read.

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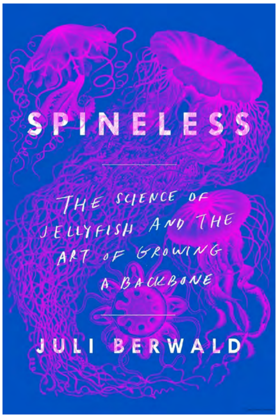
Spineless: The Science of Jellyfish and the Art of Growing a Backbone

By Juli Berwald. 2018. Riverhead Books. 352 pages, 16.00 USD, Paper.



Spineless is primarily a popular science book, with a dash of memoir thrown in for good measure. The two-part subtitle—*The Science of Jellyfish and the Art of Growing a Backbone*—reflects both elements of the writing. *The Science of Jellyfish* accounts for most of the book, and what you would expect from a well-written, well-researched non-fiction science book. The second part, *the Art of Growing a Backbone*, unfolds haltingly throughout the book, culminating in the final page of the last chapter. The memoir component is the personal story and thesis of the author, her journey to jellyfish science and speaking up for ocean health.

The author holds a Ph.D. in ocean sciences, and her interest in jellyfish stems from formative experiences during her undergraduate and graduate programs. Not a jellyfish researcher herself, the somewhat winding narrative element describes an intellectually bored writer, editor, scientist, and mother developing a burning interest in jellyfish at an age when her family vacation time could be planned to coincide with researcher interviews and fieldwork adventures. Although it can be a bit disjointed at times, the personal story of the author and the process of her enmeshment in the world of jellyfish science come together well in the last third of the book. This mix, science fact punctuated by personal moments of the author's life and experience, sets this book apart from many popular science works. Whether or not you enjoy the threads of personal narrative will likely depend on your own experiences and perspectives, but they are by no means the dominant element of the work.

Spineless is a book to suit a broad audience. It certainly has enough fascinating information, new research, and unanswered questions to satisfy interested readers. The book probes and highlights the many unknowns of jellyfish: where they grow, what they eat, and what eats them. Topics explored include jellyfish biology, ocean acidification, commercial fishing, and invasive species. Compared with other popular science works, this is a longer book, not the average short romp through a subject, and the print is small, making it longer than it looks. This allows space for interviews and research conducted over many years, all of which is meticulously cited in the "Notes" section at the end of the book.

Ostensibly organized into parts of the jellyfish life cycle—Planula, Polyp, Strobila, Ephyra, and Medusa—the writing doesn't seem to closely follow this logic, except for the last section which links to the previous pages in the author's jellyfish journey. Although a few gorgeous drawings of jellyfish life stages are included, the book would have benefitted from some additional illustration, particularly depicting the main species discussed. As it is, image-oriented readers may find themselves switching intermittently to a web browser or making notes for later. The writing quality is very good throughout. Although the feel of the writing changes in the last third or so of the book where the author includes her own and her family's personal experiences with jellyfish science and expeditions, the author's prose is easy to follow and usually descriptive enough to make up for the lack of images.

Exploring jellyfish research through the lens of a devoted hobbyist and interviewer turned collaborator, this book reveals the remarkable knowns and surprising unknowns of jellyfish and their role in the future of our oceans. It is well worth a look.

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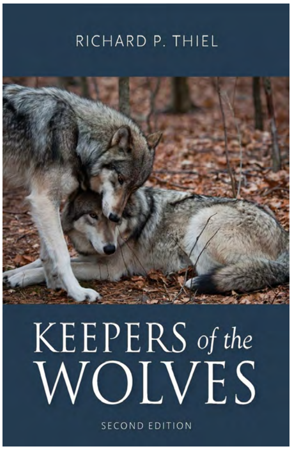
Keepers of the Wolves. Second Edition

By Richard P. Thiel. 2018. University of Wisconsin Press. 264 pages, 22.95 USD, Cloth.



Keepers of the Wolves by Dick Thiel is a very enjoyable read tracing the extirpation of Gray Wolves (*Canis lupus*) in Wisconsin, the early stages of recovery in the late 1970s–1980s, to the current recovered population of over 900 wolves inhabiting the state. This book was written by a wolf biologist, so there are great descriptions of his experiences studying wolves with numerous anecdotes of his encounters with individual wolves, especially early in the recovery process. While I may be biased because I have written a similar book of my experiences as a wildlife biologist studying Eastern Coyote/Coywolf (*Canis latrans* × *lycaon*) in Massachusetts (Way 2014), I absolutely love these kinds of books because you get to read about an animal from the person who experienced it first-hand. In this case we go back to 1978, when there had been no resident Timber Wolves (as they are called in the book) in Wisconsin for about 20 years. While packs were living nearby in bordering Minnesota, there was only the occasional sighting in Wisconsin which were surely dispersers from Minnesota. Thiel became interested in wolves when he was in high school and was determined to discover if wolves had indeed returned. In his college years, he conducted wolf track surveys in the winter-time and howling surveys over the summer to document their presence.

Thiel worked as a temporary (with no seniority accrued) biologist for the state of Wisconsin for about a decade as he led the wolf recovery team up until 1989. The book details the experiences, awe, aggravation, absurdity, and hardships (such as frigidly low temperatures) encountered as a field biologist and, unfortunately, the politics and associated public relations nightmares that go along with studying a controversial animal. We learn of individual wolves such as Big Al, Deborah, Gimpy, and Mailrunner, which he decided early in the study to name for ease of describing and remembering (pp. 95–98). I really appreciated that section given that he was a state employee at the time and naming animals is often a taboo for biologists, especially those affiliated with wildlife agencies as most would view naming as being biased in their attachment to the animals. As I discuss in Way (2014), however, I do not know how it is possible to be non-biased when you do anything that involves pouring your heart and soul into an endeavour, and recent research supports that (see Johns and Dellasalla 2017). Thiel gave great descriptions of the human-populated Wisconsin landscape when he digressed and added anecdotes on his research subjects such as when he foot-hold trapped, drugged, and then followed via radio-telemetry his study subjects by vehicle and small aircraft, cruising the many fire roads in northern, and eventually central, Wisconsin.

We also learn of humorous events which occurred during his research which is typical of any biologist's experience. While detailed throughout the book, the chapter "Murphy's Law"—which states that anything that can go wrong will go wrong—brings many of these situations to life, such as when his car key fell into a snow-bank (on a Friday afternoon no less). Or when he almost got into a plane crash on a frigid day when the plane went from barely starting to taking off with only the biologist in the plane as the pilot was outside trying to get it moving. Or when he was tracking a wolf and had to floor his vehicle through a flooded stretch of a dirt fire road. But the fun didn't end after he crossed the water, as he soon locked himself out of the car when he stopped to pick up a wolf scat he found. He ended up having to pick the lock to open the door. While these stories are certainly laugh-out-loud-while-reading-moments, they surely were quite aggravating when they were happening.

The chapter "Boy, Would I Love Your Job!" is also a bit comical. Theil started with the pretense that being a wolf biologist would be an amazing living, but then went on to describe several uncomfortable positions that he found himself in, including more than one experience talking to wolf-hating hunters at local bars. Many times, he pretended to be someone else and never revealed to his counterparts that he was the actual biologist they were complaining about. I chuckled while reading these passages. In addition to the human perspective and many cold days in the field (similar to the "Murphy's Law" chapter), the other take-home from this chapter is the fact that the bureaucracy associated with the job can make one go mad, especially when people are in a political appointment with minimal science background—aka the natural resource old boys (p. 164). I feel for Thiel, as I was not only naïve about departmental politics but also loathed its influence on decision making (p. 165), and so it is perhaps not surprising that both of us lost our research careers over it (see "They Shoot the Messenger, Don't They?" and Way 2016). Thiel's descriptions of his emotions alternating between separation anxiety and intense anger are spot on (pp. 18, 184).

I read the original version of *Keepers* back in 2001 and shared in the excitement as Thiel and his colleagues found wolf tracks in the snow, howled in the forest night and were answered back, learned to safely trap wolves to attach radio collars, and tracked the packs' ranges by air from a cramped Piper Cub. Following the stories of individual wolves and their packs as pups were born and died, when wolves were shot by accident and by intent, and ravaged by canine parvovirus and hard winters was why I loved the read. So it was with excitement that I had the opportunity to review this second edition which kept the original first 11 chapters and replaced the last three with updated information and a concluding Epilogue. This new version brings Thiel's story into the 21st century, recounting his work monitoring wolves as they spread to central Wisconsin, dealing with conflicts between wolves and landowners and recreationalists, following changes in state and federal policies, the establishment of a state wolf-hunting season in 2012, and Thiel's forecast for the future of wolves in Wisconsin. We learn that Thiel takes his first truly full-time job as an environmental educator in central Wisconsin, near his home, where wolves soon follow by returning to the Central Forest region.

By 1999 (when the first edition went to press), there were an estimated 200 Timber Wolves in 54 packs in Wisconsin. In 2017, there were an incredible 925 wolves living in 232 packs (pp. 221–222), an amazing recovery to the point where various stakeholders are polarizing wolf management. On one side are environmental groups and animal lovers suing to prevent any hunting and on the other a hyper-conservative government that took over in 2010 (pp. 206–207) and removed any semblance of science from a once prestigious wildlife department and is now closing the door to future opportunities by catering to extreme anti-environmental populism (p. 221). Perhaps Thiel's closing quote correctly summarizes the current situation of wolves in Wisconsin, "Wolves will persevere despite society's ineptitude as custodians of wildlife" (p. 228).

This book is right in my wheelhouse and I highly recommend it. If you ever want to learn about something go straight to the source. In the case of wolf recovery in Wisconsin, there could be no better person than Thiel, because he was there when wolves returned and is still around as wolves have recovered to the point of being the most abundant that they have been on Wisconsin's landscape in well over a century.

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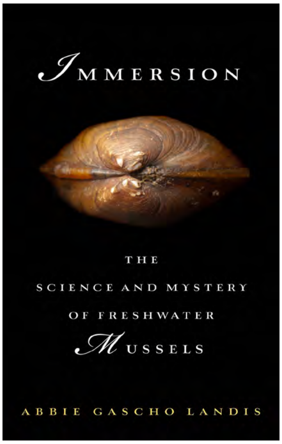
Immersion: The Science and Mystery of Freshwater Mussels

By Abbie Gascho Landis. 2017. Island Press. 256 pages, 34.50 CAD, Cloth or E-book.



Immersion is a book about freshwater mussels: what they are, how they live, why they matter, why so many of them are imperilled, and how we can change that. Best described as a popular science book, this is no sterile examination of freshwater bivalves. The writing is funny and charming, equal parts accurate, informative description, and transportive narration. In addition to presenting a compelling argument for why freshwater mussels are fascinating creatures, *Immersion* explores tensions between water for crop irrigation and water to keep the river flowing, the *Endangered Species Act* versus corporate interests, and mussel researchers versus the onslaught of pollution, habitat loss, and fragmented landscapes.

A self-professed freshwater mussel groupie, the author is a writer, veterinarian, and naturalist. She is also the wife of a freshwater mussel biologist and the mother of two creek-loving toddlers. Sourced from field and laboratory visits with experts as well as her own musseling experiences, the ten chapters are well organized and coherent, covering mussel reproduction, research, and restoration in engrossing detail. The selected bibliography provides further reading for the dedicated enthusiast, including peer-reviewed journal articles from the scientists whose work is featured in the text as well as news pieces and reference texts. Individual chapter sections vary in length but none are overlong or feel bloated. As each section is a logical and relatively self-contained parcel nested within the chapter's thematic whole, the structure of the book lends itself both to casual and to binge reading styles. The line drawings peppered throughout the book are few but effective, illustrating key details in harmony with the text. The author's prose is appropriately descriptive and I was certainly not left wanting for illustrations to visualize the subject matter.

This book ignites a sudden and urgent impulse to grab a snorkel and run to the nearest riffle. If you live in northern latitudes, I recommend reading *Immersion* in the early warm weather months, so that you can satisfy that urge when mussels are active (and without the need for a polar bear dip). It is the quality of writing and depth of enthusiasm for the topic that sets this book apart from other similar popular science books. Instead of passively informing the reader about an interesting topic, the author and the researchers within the pages carry you with them into their streams and laboratories. Like them, you may catch yourself proselytizing about mussel biology to friends and strangers alike.

This is not a book you will want to part with, instead revisiting it from time to time to refresh and revisit. If you are new to the world of freshwater mussels, this book is guaranteed to change the way you look at your local creeks, rivers, and streams. I can (and do) enthusiastically recommend this book to anyone with so much as a glimmer of interest in the natural world.

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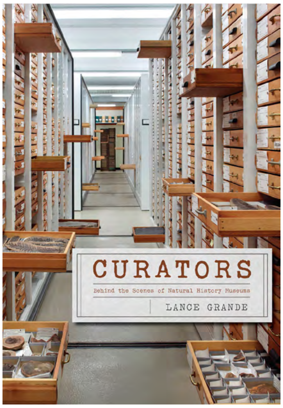
OTHER

Curators: Behind the Scenes of Natural History Museums

By Lance Grande. 2017. University of Chicago Press. 432 pages, 35.00 USD, Cloth, 21.50 USD, E-book.



Museums are, perhaps, best known for exhibitions. When visitors walk into any major museum, galleries and exhibits are the first things they see so it's easy to assume that these are the museums' main function. True, museums are about exhibitions, but they are also about so much more. Museums collect, conserve, communicate, and research, in addition to developing displays. In fact, most large museums have only a fraction of their collections on display. Much of a museum's activity goes on behind the scenes, in the research and collecting by curators. Their projects often provide content for exhibitions, in the form of spectacular specimens and their associated stories. However, curators' work remains essentially unknown by museum visitors. Lance Grande explores this unknown realm in *Curators*, his behind the scenes examination of curatorship.

So what, exactly, does a curator do? "I came to realize that few people understood what a natural history museum curator does", writes Grande in his Preface (p. ix). I smiled wryly as I read his lament because I too have received blank looks when I have told people I am a museum curator. It's not a career that's well known, though it is one that can be filled with interest, variety, and opportunities, as Grande's life story well shows. According to his succinct definition, a natural history curator is a "research scientist whose job is to bring authority and originality to their museum's scientific message" (pp. ix–x). Curators accomplish this through "original research" and the dissemination of "knowledge of scientific discoveries to students, other scientists, and the general public" (p. x). Interestingly, Grande's definition does not include developing natural history collections, though those collections derive in part from research activities, in particular fieldwork. Building and caring for collections are usually significant components of the job description and occupy much of a curator's time. Nevertheless, much of Grande's narrative does in fact focus on collections, how they are acquired, used, displayed, and maintained for the future. For anyone who has donated natural history specimens to a museum, this book provides insights about what happens to them and how they may be used.

Working for one of North America's major museums, Grande has had many opportunities for research, travel, and participation in diverse projects. His account is arranged roughly chronologically, following his career from a student interested in fossils to a senior museum administrator. Grande is primarily a palaeontologist with a focus on the fossil record and the history of life. Thus, much of his narrative, especially in the earlier chapters which deal with his education and early career experience, describes his fieldwork and collecting. His research focus has been fossil fishes, chiefly those from the Green River Formation in Wyoming. He proudly records that he has worked in his field area for 41 field seasons, as of 2015 (p. 63). Later in his career, he moved into more administrative roles, which were accompanied by different sets of challenges. His focus increasingly shifted from research to management, including issues management, balancing staffing and programs, and securing funding and outside support for specific projects. This progression gives him the opportunity to talk about many aspects of a curator's life, including dealing with some of the ethical and practical issues around collecting and collections.

For many readers, the Field Museum in Chicago will perhaps be best known as the home of SUE the T-rex, who features prominently in the museum's promotional imagery and who even has a snark-rich Twitter account. The story behind the Field Museum's acquisition of SUE is lengthy, complicated, and fascinating, highlighting the difficult issues that arise when specimens of high scientific value also have high commercial value. As the most complete *Tyrannosaurus rex* found to that time (1990), SUE's ownership was contested from the beginning, an acrid controversy only resolved in court. Thereafter, the fossil's sale generated global interest, tension, and media hype. On 4 October 1997, Sotheby's sold the specimen to the Field Museum in a nail-biting auction. Securing SUE cost the museum more than eight million dollars (p. 133).

Although this specimen was secured for a major museum that recognized its tremendous display potential, scientific significance, and educational value, the story does raise questions about the commercialization of fossils. Grande argues that commercial fossil quarries are important to museums and points out that his own work on fossil fishes, in Wyoming and Mexico, was facilitated by cooperation with commercial fossil extraction. He reasons that some localities "could not possibly be adequately sampled for scientific study without the help of amateur and responsible commercial interests" (p. 43). On the other hand, many fossils are found purely opportunistically through industrial, mining, and development activities. Specimens may be revealed when large-scale disturbances expose fossil-bearing bedrock or sediments. A recent exhibition, "Grounds for Discovery", at the Royal Tyrrell Museum in Alberta highlighted exactly these kinds of chance finds. Good collaborative relationships can result in serendipitous specimens becoming part of museum collections.

Collaborative work also happens across disciplines. Grande describes one such long-term fruitful collaboration in his career, with an ichthyologist, Wally Bemis from the University of Massachusetts, who studies modern rayfin fishes. Their fields of expertise are complementary: Grande on skeletal anatomy, and Bemis on soft tissue anatomy. Studying modern fish specimens helped Grande to understand the structures he was seeing in the fossil record. Bemis obtained many specimens through donation at an annual marine fishing tournament off the coast of Alabama, which Grande describes as "a boon to fish research" (p. 96). Bemis ran a contest for "Most Unusual Fish" and through this and a filleting service was able to secure many large, rare, or unusual fish specimens. Besides enhancing the Field Museum's collection, specimens also went to other museums, universities, and institutions. Collections come from many sources, some not so obvious!

Notwithstanding his focus on palaeontology, Grande introduces the other curatorial programs at the Field Museum. On the natural history side, the museum supports curators in botany, lichenology, ornithology, geology, meteoritics, marine invertebrate zoology, and entomology. The museum also supports several human history curators, including those focussed on cultural anthropology, archaeology, ethnology, and physical anthropology. This reflects the traditional subdivision of most large museums into natural history and human history sections. Field Museum curators travel to all parts of the globe. Grande mentions research projects that have taken place in Israel, Russia, Mexico, and many other countries in Europe and Asia. Grande emphasizes that interdisciplinary work at the museum is facilitated by the relatively small number of curators, 21 in 2014 (p. 158), and that the closeness of the group often leads to fruitful collaborations. This echoes my own experience as a curator. Many Field curators also mentor and supervise graduate students and thereby train the next generation of researchers and curators. Being a natural history curator is indeed a multifaceted job!

Museum collections aren't "owned" by curators; they are preserved and handed down from curator to curator. This means that specimens are available for re-investigation when new analytical techniques become available. Grande provides a particularly noteworthy example of this in the story of the "Man-eaters of Tsavo". These lions terrorized rail constructions crews in Kenya in 1898 until they were shot and killed by John H. Patterson, who later sold the skins and skulls to the Field Museum, where the taxidermied specimens went on display in 1926. In the early 2000s, the Mammals curator, Bruce Patterson (no relation to the hunter) re-examined the skulls. He found that one of the lions had severe dental problems that undoubtedly caused pain and difficulty catching and killing regular prey. Hence the animal probably turned to the easier caught and killed railway workers as a food source. Grande also points out that the century between collection and re-examination also spans a substantive change in attitude towards wildlife and "Big Game". Nowadays, Field Museum curators are heavily involved in conservation efforts for wildlife and ecosystems in many areas of the world.

Curators may also participate in exhibit development, which can provide a tremendous outlet for creativity and originality. With extensive collections across natural history and great depth of expertise, there is usually no lack of high-quality specimens and story ideas. Natural history lends itself well to display. What is challenging is telling these stories and displaying the specimens in a way that is meaningful and engaging to visitors. This requires attention to the scientific importance of the material together with other qualities such as beauty. Grande emphasizes the aesthetic gaze when describing his contribution to the re-development of a gallery showcasing gemstones and jewelry. Exhibit development requires collaboration between curators and professionals with different skills, such as designers, educators, and fabricators. When this succeeds, the results can be breathtaking.

For anyone interested in natural history collections, Grande's account is a great read—lucid, entertaining, and informative. The book is beautifully produced with a clear font on high quality paper. With its modest $35 price, it is exceptional value for a high-end hardback book. Notably, it contains abundant colour images. Each chapter is followed by a half-dozen or more pages of colour images that directly relate to its topic, ending with an image that serves as an introduction to the next chapter. I really enjoyed this interweaving of the narrative and images. It was extremely effective in reinforcing the messages of the text. I especially liked the images of specimens that Grande has collected and studied and the pictures of his field crews. These show that the collections are a collective effort and the efforts of many people are involved in their curation and long-term preservation. Without field assistants and skilled preparators back in the lab, museum collections would not be accessible for research or display and the research opportunities for curators would be limited. Although Grande's book is focussed on his career as a curator, his ultimate message is that the museum is an institution that benefits from the skill and dedication of many professionals from different fields.

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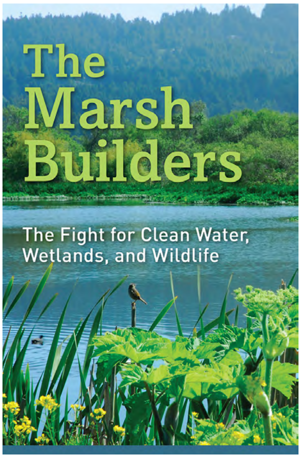
The Marsh Builders: The Fight for Clean Water, Wetlands, and Wildlife

By Sharon Levy. 2018. Oxford University Press. 248 pages, 39.95 CAD, Cloth. Also available as an E-book.



The Marsh Builders, a book about constructed wetlands? Well not exactly, but that appears to be what inspired Sharon Levy to embark on this historical account of human waste, wetland destruction, and the United States' *Clean Water Act* (CWA). The actual "marsh building" doesn't start until around halfway through the book!

Humanity's relationship with the environment has changed dramatically over the past 200 years. We all know this, but to write a book that documents our history from the perspective of human waste, wetlands, and water pollution is unique. Levy has obviously done extensive research; in fact, there is an extensive list of numbered references at the end of each chapter. As a result, the book provides an insightful and vivid account of the science and politics of dealing with a very real problem—what to do with human waste as cities like London and Berlin develop with populations of over a million people and growing. Piping waste to the nearest watercourse is fine, until your neighbours downstream become ill. The book draws the reader in with the first chapter, "Cholera's Frontiers", set in London, England, around 1850.

Chapters 2 and 3, "The Tides of Change" and "The Microbe Solution", document our evolving understanding of disease and its link to human waste. Initially disease was thought to arise from miasma, or the stench of human waste, but new tools, such as the microscope, and scientific approaches to treating human waste, such as the activated sludge process discovered in 1914, began to inform the politics of urban planning. Elected officials, then as now, were responsible for public well-being and, working with limited funds and the best knowledge of the day, approved infrastructure projects to deal with human waste. The CWA created in 1971 transferred authority over sewage and industrial effluent regulation from individual states to the federal Environmental Protection Agency (EPA), mandating "a wildly idealistic goal that all such discharges into US waters should cease by 1985" (p. 75). To this day, individuals living in cities simply flush the toilet and turn on the tap for clean water, with little thought of the long and continuing struggle to make this system work. Herein lies the heart of *The Marsh Builders*, the tension between science, politics, and human waste.

Chapter 6 describes "Fighting the Big Machine"—aka the Humboldt Bay Wastewater Authority (HBWA)—versus the small-town politics, petitions, committees, and legal battles that delayed conventional approaches to wastewater treatment long enough for a treatment alternative to emerge that would be replicated around the world. Levy gives a detailed account of the small, feisty town of Arcata, located on the Pacific coast of northern California, and its fight with the HBWA. It's a classic story of David fighting Goliath: big government with federal funding intended to build a sewage treatment megaproject connecting small towns with a pipe running under Arcata Bay to a regional treatment plant on Humboldt Bay. Each town along the route was expected to join the project, including making enormous, sometimes bankrupting, financial contributions to building and maintaining the infrastructure.

Arcata had a different vision for wastewater treatment: a low cost, low energy, local solution using open surface water wetlands that would meet CWA guidelines, create wildlife habitat, and improve the ecology of Humboldt Bay. However, this had never been done before and few believed it would work. It was a fight against the bureaucratic and engineering status quo, and Arcata won in the end. But with the wetlands now almost 40 years old and losing their capacity to treat the ever-increasing volume of sewage, Arcata once again finds itself up against an "engineered" solution versus the original treatment wetlands now rich in native biodiversity.

As an ecologist, it is painful to read Chapter 7, "The United States of Vanished Wetlands", that documents the once great bounty and biodiversity of coastal and inland wetlands in America that were demonized for health reasons, hated because they could not be traversed, and deemed unproductive until drained. *The Marsh Builders* details what early colonizers faced in America and describes how society's perception of wetlands, disease, and pollution have changed over time. The once Great Black Swamp, a wetland over 4000 km^2 in size, was a major impediment for people moving westward and seen as a breeding zone for mosquitos until it was drained and converted to farmland. Today, flooding and non-point sources of agricultural pollution causing toxic algal blooms in rivers and lakes have society revisiting their relationship with the Black Swamp, with calls to return 10% of the landscape to wetland.

The Marsh Builders also documents the introduction and rise of new exotic diseases associated with wetlands, such as malaria and yellow fever, which were brought to America with colonization. When science identified mosquitos as the insect vector for these diseases, government in its bid to protect citizens institutionalized the draining of wetlands and in the 1940s promoted the use of organochlorine pesticides such as DDT. Few drained wetlands are restored today, but fortunately where habitat is available wildlife is recovering following a ban on the use of DDT in 1972.

The last chapter of the book, "The Fight This Time", highlights the fact that, while it is well known that non-point sources of pollution (mainly from agriculture) cause over 75% of rivers and lakes to fail water quality standards, the CWA exempts farmers from their standards. And the momentum building in the EPA to regulate non-point sources of pollution has been derailed by Scott Pruitt, appointed by President Trump to head the EPA. While writing this review, I learned that Pruitt resigned as head of the EPA in December 2018. He will be replaced by Andrew Wheeler, a former coal lobbyist, dramatically highlighting the continuing saga of the tension between science, politics, and the world we choose to live in. *The Marsh Builders* is probably not the best title for the book, but that shouldn't stop you from reading this excellent account of our relationship with water and wetlands over the past 200 years by veteran science journalist Sharon Levy.

BRENT TEGLER

Liana Environmental Consulting Ltd., Fergus, ON, Canada

NEW TITLES

Prepared by Barry Cottam

Please note: Only books marked † or * have been received from publishers. All other titles are listed as books of potential interest to subscribers. Please send notice of new books—or copies for review—to the Book Review Editor.

†Available for review *Assigned

Currency Codes: CAD Canadian Dollars, USD US Dollars, EUR Euros, AUD Australian Dollars, GBP British Pound.

BOTANY

The Grasses of Florida. By David W. Hall. 2019. University Press of Florida. 528 pages, 80.00 USD, Cloth.

Managing the Wild: Stories of People and Plants and Tropical Forests. By Charles M. Peters. 2018. Yale University Press. 208 pages, 30.00 USD, Cloth.

The Natural History of Flowers. By Michael Fogden and Patricia Fogden. 2018. Texas A&M University Press. 232 pages, 37.00 USD, Cloth. Also available as an E-book.

Unnatural Texas? The Invasive Species Dilemma. By Robin W. Doughty and Matt Warnock Turner. 2019. Texas A&M University Press. 272 pages, 32.00 USD, Cloth.

ENTOMOLOGY

Bedbug. By Klaus Reinhardt. 2018. Reaktion Books. Distributed by University of Chicago Press. 192 pages, 19.95 USD, 12.95 GBP, Paper.

The Biota of Canada – A Biodiversity Assessment. Part 1: The Terrestrial Arthropods. By David W. Langor and Cory Sheffield. 2019. ZooKeys, Issue 819. 520 pages, 99.00 GBP, Paper. Open access at https://zookeys.pensoft.net/issue/1251/.

Cerambycidae (Coleoptera) of Canada and Alaska. By Yves Bousquet, Serge Laplante, H.E. James Hammond, and David W. Langor. 2017. Entosphinx. 300 pages, 180.00 EUR, Cloth.

Dragonfly Nymphs of North America: An Identification Guide. By Kenneth Tennessen. 2019. Springer. 588 pages and 936 illustrations, 279.99 USD, Cloth, 219.00 USD, E-book.

Edible Insects and Human Evolution. By Julie Lesnik. 2018. University Press of Florida. 208 pages, 79.95 USD, Cloth.

Innumerable Insects. By Michael S. Engel. Foreword by Tom Baione. 2018. American Museum of Natural History and Sterling Publishing. 232 pages, 27.95 USD, Cloth.

Never Home Alone: From Microbes to Millipedes, Camel Crickets, and Honeybees, the Natural History of Where We Live. By Rob Dunn. 2018. Basic Books. 336 pages, 36.50 CAD, Cloth, 23.99 CAD, E-book.

Why Every Fly Counts: A Documentation about the Value and Endangerment of Insects. Fascinating Life Sciences Series. By Hans-Dietrich Reckhaus. 2017. Springer. 111 pages, 39.99 USD, Cloth.

Underbug: An Obsessive Tale of Termites and Technology. By Lisa Margonelli. 2018. Scientific American/Farrar, Straus and Giroux. 320 pages, 27.00 USD, Cloth, 16.00 USD, Paper, 13.99 USD, E-book.

HERPETOLOGY

Cane Toad Wars. By Rick Shine. Foreword by Harry W. Greene. 2018. University of California Press. 288 pages, 34.95 USD, Cloth or E-book.

†Ecology and Conservation of the Diamond-Backed Terrapin. Edited by Willem M. Roosenburg and Victor S. Kennedy. 2019. Johns Hopkins University Press. 296 pages, 79.95 USD, Cloth or E-book.

Turtles in Trouble: The World's 25+ Most Endangered Tortoises and Freshwater Turtles – 2018. Presented by the Turtle Conservation Coalition. 2018. Turtle Conservancy. 84 pages, 10.00 USD, Cloth. Free PDF available at http://www.iucn-tftsg.org/turtles-in-trouble-2018/.

ICHTHYOLOGY

Atlantic Cod: A Bio-Ecology. Edited by George Rose. 2019. Wiley-Blackwell. 416 pages, 219.99 CAD, Cloth, 175.99 CAD, E-book.

Fishes of the Western North Atlantic. Memoir I: Sears Foundation for Marine Research. Volumes

1–10. 2018. Yale University Press. Various pagination, 75.00 USD each, Paper.

The Life of the Lakes: A Guide to the Great Lakes Fishery. Fourth Edition. By Brandon C. Schroeder, Dan M. O'Keefe, and Shari L. Dann. 2019. University of Michigan Press. 136 pages, 19.95 USD, Paper.

ORNITHOLOGY

Birds of Saskatchewan. Manley Callin Series No. 8. By Alan R. Smith, C. Stuart Houston, and J. Frank Roy. 2019. Nature Saskatchewan. 768 pages, 79.95 CAD, Cloth.

A Fieldworker's Guide to the Golden Eagle. By Dave Walker. 2017. Whittles Publishing. 248 pages and 16-page colour section, 19.99 GBP, Paper, 13.99 GBP, E-book.

Long Hops: Making Sense of Bird Migration. By Mark Denny. 2016. University of Hawaii Press. 256 pages, 65.00 USD, Cloth, 29.99 USD, Paper.

The Population Ecology and Conservation of Charadrius Plovers. Edited by Mark A. Colwell and Susan M. Haig. 2019. CRC Press (Taylor & Francis Group). 336 pages, 149.95 USD, Cloth.

Taking Flight: A History of Birds and People in the Heart of America. By Mark Edmonds. 2018. Wisconsin Historical Society Press. 304 pages, 28.95 USD, Paper. Also available as an E-book.

Shorebirds in Action: An Introduction to Waders and their Behaviour. By Richard Chandler. 2017. Whittles Publishing. 256 pages and 440 colour illustrations, 21.95 GBP, Paper.

ZOOLOGY

The First Domestication: How Wolves and Humans Coevolved. By Raymond Pierotti and Brandy R. Fogg. 2017. Yale University Press. 344 pages, 38.00 USD, Cloth.

End of the Megafauna: The Fate of The World's Hugest, Fiercest, and Strangest Animals. By Ross D.E. MacPhee. Illustrated by Peter Schouten. 2018. W.W. Norton. 256 pages, 35.00 USD, Cloth.

†Mama's Last Hug: Animal and Human Emotions. By Frans de Waal. 2019. W.W. Norton. 336 pages, 36.95 USD, Paper.

Pandas to Penguins: Ethical Encounters with Animals at Risk. By Melissa Gaskill. 2018. Texas A&M University Press. 256 pages, 28.00 USD, Flexbound. Also available as an E-book.

***Return of the Wolf: Conflict & Coexistence.** By Paula Wild. 2018. Douglas & McIntyre. 272 pages, 32.95 CAD, Cloth.

Why Big Fierce Animals Are Rare: An Ecologist's Perspective. By Paul A. Colinvaux. With a new foreword by Cristina Eisenberg. 2018. Princeton University Press. 272 pages, 18.95 USD, Paper. First published in 1979.

The Wisdom of Wolves: Lessons from the Sawtooth Pack. By Jim Dutcher and Jamie Dutcher. Foreword by Marc Bekoff. 2018. National Geographic Society. 224 pages, 26.00 USD, Cloth.

OTHER

***A Year on the Wild Side: A West Coast Naturalist's Almanac.** By Briony Penn. 2019. TouchWood Editions. 400 pages, 26.00 CAD, Cloth.

Abundant Earth: Toward an Ecological Civilization. By Eileen Crist. 2019. University of Chicago Press. 288 pages, 105.00 USD, Cloth, 35.00 USD, Paper. Also available as an E-book.

The Art of Naming. By Michael Ohl. Translated by Elisabeth Lauffer. 2018. MIT Press. 312 pages, 29.95 USD, Cloth.

Big Lonely Doug. By Harley Rustad. 2018. House of Anansi Press, Walrus Books. 328 pages, 22.95 CAD, Paper.

The Birth of the Anthropocene. By Jeremy Davies. 2018. University of California Press. 248 pages, 29.95 USD, Cloth, 27.95 USD, Paper or E-book.

The Boatman: Henry David Thoreau's River Years. By Robert M. Thorson. 2019. Harvard University Press. 336 pages, 17.95 USD, Paper.

Bombs Away: Militarization, Conservation, and Ecological Restoration. By David G. Havlick. 2018. University of Chicago Press. 208 pages, 35.00 USD, Cloth. Also available as an E-book.

Collecting the World: Hans Sloane and the Origins of the British Museum. By James Delbourgo. 2019. Harvard University Press – Belknap Press. 544 pages, 18.95 USD, Paper.

***Darwin Comes to Town: How the Urban Jungle Drives Evolution.** By Menno Schilthuizen. 2018. Picador. 304 pages, 27.00 USD, Cloth.

The Demon in the Machine: How Hidden Webs of Information Are Finally Solving the Mystery of Life. By Paul Davies. 2019. Allen Lane. 272 pages, 42.95 CAD, Cloth.

Discerning Experts: The Practices of Scientific Assessment for Environmental Policy. By Michael Oppenheimer, Naomi Oreskes, Dale Jamieson, Keynyn Brysse, Jessica O'Reilly, Matthew Shindell, and Milena Wazeck. 2019. University of Chicago Press. 304 pages, 90.00 USD, Cloth, 35.00 USD, Paper or E-book

Ecology and Power in the Age of Empire: Europe and the Transformation of the Tropical World. By Corey Ross. 2017. Oxford University Press. 512 pages, 61.00 CAD, Cloth. Also available as an E-book.

The Evolving Animal Orchestra: In Search of What Makes Us Musical. By Henkjan Honing. Translated by Sherry MacDonald. 2019. MIT Press. 160 pages, 27.95 USD, Cloth.

Extreme Conservation: Life at the Edges of the World. By Joel Berger. 2018. University of Chicago Press. 368 pages, 30.00 USD, Cloth, 18.50 USD, E-book.

Dreamers, Visionaries, and Revolutionaries in the Life Sciences. Edited by Oren Harman and Michael R. Dietrich. 2018. University of Chicago Press. 336 pages, 120.00 USD, Cloth, 40.00 USD, Paper. Also available as an E-book.

Drawn to the Deep. The Remarkable Underwater Explorations of Wes Skiles. By Julie Hauserman. 2018. University Press of Florida. 256 pages, 24.95 USD, Cloth.

Enlivenment: Toward a Poetics for the Anthropocene. Untimely Meditations Series. By Andreas Weber. 2019. MIT Press. 208 pages, 15.95 USD, Paper.

The Epochs of Nature. By Georges-Louis Leclerc, le comte de Buffon. Translated and edited by Jan Zalasiewicz, Anne-Sophie Milon, and Mateusz Zalasiewicz. Introduction by Jan Zalasiewicz, Sverker Sörlin, Libby Robin, and Jacques Grinevald. 2018. University of Chicago Press. 288 pages, 45.00 USD, Cloth. Also available as an E-book. First published in 1778.

Fire in California's Ecosystems. Second Edition. Edited by Jan W. van Wagtendonk, Neil G. Sugihara, Scott L. Stephens, Andrea E. Thode, Kevin E. Shaffer, and Jo Ann Fites-Kaufman. Foreword by James K. Agee. 2018. University of California Press. 568 pages, 120.00 USD, Cloth or E-book.

Georg Forster: Voyager, Naturalist, Revolutionary. By Jurgen Goldstein. 2019. University of Chicago Press. 240 pages, 45.00 USD, Cloth or E-book.

***The Great Himalayan National Park: The Struggle to Save the Western Himalayas.** By Anthony J. Gaston and Sanjeeva Pandey. 2019. Niyogi Books. 364 pages, 280 colour pictures, and 15 maps, 52.20 CAD, Cloth.

Imagining Extinction: The Cultural Meanings of Endangered Species. By Ursula K. Heise. 2016. 288 pages, 82.50 USD, Cloth, 27.50 USD, Paper. Also available as an E-book.

Levelling the Lake: Transboundary Resource Management in the Lake of the Woods Watershed. By Jamie Benidickson. 2019. University of British Columbia Press. 367 pages, 89.95 CAD, Cloth.

Magnetic North: Sea Voyage to Svalbard Wayfarer. By Jenna Butler. 2018. University of Alberta Press. 120 pages, 19.99 CAD / USD, Paper or PDF.

Marine Historical Ecology in Conservation: Applying the Past to Manage for the Future. Edited by J.N. Kittinger, L.M. McClenachan, K.B. Gedan, and L.K. Blight. 2014. University of California Press. 312 pages, 45.00 USD, Cloth. Also available as an E-book.

Moths, Myths, & Mosquitoes. The Eccentric Life of Harrison G. Dyar, Jr. By Marc E. Epstein. 2016. Oxford University Press. 360 pages, 42.95 CAD, Cloth. Also available as an E-book.

Nonsense on Stilts: How to Tell Science from Bunk. Second Edition. By Massimo Pigliucci. 2018. University of Chicago Press. 336 pages, 22.50 USD, Paper. Also available as an E-book.

Serendipity: An Ecologist's Quest to Understand Nature. By James A. Estes. Foreword by Harry W. Greene. 2016. University of California Press. 256 pages, 29.95 USD, Cloth or E-book

The Secret Wisdom of Nature: Trees, Animals, and the Extraordinary Balance of All Living Things – Stories from Science and Observation. Third volume in The Mysteries of Nature Trilogy. By Peter Wohlleben. Translated by Jane Billinghurst. 2019. Greystone Books. 272 pages, 29.95 CAD, Cloth.

A Theory of Global Biodiversity (MPB-60). By Boris Worm and Derek P. Tittensor. 2018. Princeton University Press. 232 pages, 49.95 USD, Cloth or E-book.

Wildlife and Wind Farms – Conflicts and Solutions. Volume 1, Onshore: Potential Effects. Edited by Martin Perrow. 2017. Pelagic Publishing. 298 pages, 40.00 GBP, 69.06 CAD, Paper.

Wildlife and Wind Farms – Conflicts and Solutions. Volume 2, Onshore: Monitoring and Mitigation. Edited by Martin Perrow. 2017. Pelagic Publishing. 227 pages, 40.00 GBP, 69.06 CAD, Paper.

Wildlife and Wind Farms – Conflicts and Solutions, Volume 3. Offshore: Potential Effects. 2019. Edited by Martin Perrow. 2019. Pelagic Publishing. 301 pages, 45.00 GBP, 77.69 CAD, Paper.

Woodland Survey Handbook: Collecting Data for Conservation in British Woodland. By Keith Kirby and Jeanette Hall. 2019. Pelagic Publishing. 220 pages, 30.00 GBP, 51.79 CAD, Paper.

News and Comment

Upcoming Meetings and Workshops

Eastern Bird Banding Association Annual Meeting

The 96th annual meeting of the Eastern Bird Banding Association to be held 12–14 April 2019 in Rochester, New York. Registration is currently open. More information is available at https://ebba2019.com/.

Northeast Natural History Conference

The 19th Northeast Natural History Conference to be held 12–14 April 2019 at the Sheraton Springfield Hotel, Springfield, Massachusetts. Registration is currently open. More information is available at https://www.eaglehill.us/NENHC_2019/NENHC2019.shtml.

Northeast Fish & Wildlife Conference

The 75th annual Northeast Fish & Wildlife Conference, hosted by the Connecticut Department of Energy & Environmental Protection, to be held 14–16 April 2019 at the Mystic Marriott Hotel, Groton, Connecticut. Registration is currently open. More information is available at https://www.neafwa.org/conference.html.

Entomological Society of America, Southwestern Branch Meeting

The 67th annual meeting of the Southwestern Branch of the Entomological Society of America to be held 14–18 April 2019 at the Hyatt Regency Tulsa, Tulsa, Oklahoma. Registration is currently open. More information is available at https://www.entsoc.org/southwestern/2019-branch-meeting.

Canadian Society of Zoology Annual Meeting

The annual meeting of the Canadian Society of Zoology to be held 13–17 May 2019 at the St. Clair College Centre of the Arts, Windsor, Ontario. Registration is currently open. More information is available at https://csz-scz2019.com/.

Society for Freshwater Science Annual Meeting

The annual meeting of the Society for Freshwater Science to be held 19–23 May 2019 at the Salt Palace Convention Center, Salt Lake City, Utah. Registration is currently open. More information is available at https://sfsannualmeeting.org/.

Society of Wetland Scientists' Annual Meeting

The Society of Wetland Scientists' Annual Meeting to be held 28–31 May 2019 at the Hilton Baltimore, Baltimore, Maryland. The theme of the conference is: 'The Role of Wetlands in Meeting Global Environmental Challenges: Linking Wetland Science, Policy, and Society'. Registration is currently open. More information is available at https://www.swsannualmeeting.org/.

International Urban Wildlife Conference

The International Urban Wildlife Conference to be held 2–5 June 2019 at Portland State University, Portland, Oregon. The theme of the conference is: 'Collaboration & Conservation: Applications to Urban Wildlife'. Registration is currently open. More information is available at http://www.urban-wildlife.org/.

Conference on Great Lakes Research

The 62nd annual Conference on Great Lakes Research, hosted by The College at Brockport, to be held 10–14 June 2019 at The College at Brockport, State University of New York, Brockport, New York. The theme of the conference is: 'Large Lakes Research: Connecting People and Ideas'. Registration is currently open. More information is available at http://iaglr.org/iaglr2019/.

North American Moose Conference & Workshop

The 53rd annual North American Moose Conference & Workshop to be held 10–14 June 2019 at the Sugarloaf Resort, Carrabassett Valley, Maine. Registration is currently open. More information is available at https://www.namoose19.com/.

Phycological Society of America Annual Meeting

The annual meeting of the Phycological Society of America to be held 23–27 June 2019 at the Hollywood Beach Marriott, Fort Lauderdale, Florida. Registration is currently open. More information is available at https://www.psaalgae.org/meetings/2019/6/27/psa-2019-annual-meeting.

American Ornithology 2019

The 137th annual meeting of American Ornithology and the 3rd annual meeting of the American Ornithological Society to be held 24–28 June 2019 at the William A. Egan Civic and Convention Center, Anchorage, Alaska. The theme of the conference is: 'Birds on the Edge: Dynamic Boundaries'. Registration is currently open. More information is available at https://amornithmeeting.org/.

American Society of Mammalogists Annual Meeting

The Centennial Celebration and 99th annual meeting of the American Society of Mammalogists to be held 28 June–2 July 2019 at the Hyatt Regency Washington, Washington, DC. Registration is currently open. More information is available at https://www.mammalmeetings.org/.

Release of Flora of Newfoundland and Labrador webpage

A comprehensive treatment of the vascular flora of Newfoundland and Labrador was posted online by Susan J. Meades and William J. Meades in late 2018: https://newfoundland-labradorflora.ca. It is based on the authors' decades of experience on "The Rock", as well as the borrowed expertise of other local and "From Away" field botanists. All species, subspecific taxa, and named hybrids known from here are listed and a statement on their status is provided. Technical descriptions of some taxa are included with the expectation, over time, of providing this feature for all species in the *Flora*. Keys to the species of all major families are included as are exhaustive enumerations of synonyms. The latter may seem out of place in a regional study but the complex taxonomic history of this area's flora—particularly in light of the prolific taxonomic publication of "splitters" like M.L. Fernald and associations in the early 20th Century—make this a valuable addition. This independently supported, constantly updating floristic resource will be of great value to all field botanists active or interested in this area.

DANIEL F. BRUNTON
Ottawa, ON, Canada

Editors' Report for Volume 131 (2017)

Mailing dates for the four issues in volume 131 are as follows: 30 August 2017, 1 December 2017, 28 June 2018, and 11 April 2018. Summaries of the distribution of memberships in the Ottawa Field-Naturalists' Club, who all receive access to *The Canadian Field-Naturalist*, and subscribers to *The Canadian Field-Naturalist* for 2017 are provided in Table 1, along with comparison numbers for volume 130. Institutional subscribers potentially represent many thousands of users. The number of articles published in volume 131 declined over the number published in volume 130 but the number of notes remained about the same (Table 2); birds and mammals were the main subject areas (Table 2). A new type of manuscript, thematic collections, began to be published in 2017; these are editor-selected compilations of previously-published contributions in both *The Canadian Field-Naturalist* and the regional Ottawa Field-Naturalists' Club publication, *Trail & Landscape*, on a central theme. The number of book reviews and new titles published in volume 131 more than doubled and tripled, respectively, over the numbers in volume 130 (Table 3). The total number of pages published increased slightly for volume 131 over volume 130 (Table 4), with articles and notes contributing most to the page count although there was a decrease in the number of pages for articles as would be expected with six fewer articles being published (Table 2).

Table 2. Number of research articles and notes published in *The Canadian Field-Naturalist*, volume 131 (volume 130), by major field of study. Two thematic collections, one on alvars in Canada and the other on documenting species new to Canada, also were published in volume 131.

Subject	Articles	Notes	Total
Mammals	3 (9)	8 (10)	11 (19)
Birds	10 (4)	6 (5)	16 (9)
Amphibians and Reptiles	3 (4)	2 (0)	5 (4)
Fishes	1 (4)	2 (2)	3 (6)
Plants	3 (4)	2 (1)	5 (5)
Insects	1 (2)	0 (0)	1 (2)
Non-insect Invertebrates	2 (3)	1 (2)	3 (5)
Other	1 (0)	0 (0)	1 (0)
Total	24 (30)	21 (20)	45 (50)

Table 3. Number of reviews and new titles published in the Book Review section of *The Canadian Field-Naturalist*, volume 131 (volume 130), by topic.

	Reviews	New Titles
Zoology	15 (10)	155 (45)
Botany	7 (3)	43 (16)
Miscellaneous	18 (9)	111 (32)
Total	40 (22)	309 (93)

A number of new initiatives began with volume 131 in addition to the thematic collections. Beginning with issue 1, *The Canadian Field-Naturalist* had digital object identifiers (DOIs) automatically assigned to all published content via the Online Journal System. The DOI is a global system that provides a persistent link for digital content to a location on the internet. This system requires that all references cited within a manuscript also are identified with a DOI (providing they have one). Many older issues of *The Canadian Field-Naturalist* do not have DOIs but, to promote all previously published content in *The Canadian Field-Naturalist* available through the Biodiversity Heritage Library (BHL), the URL web address for each is added to the reference. All volumes of *The Canadian Field-Naturalist* more than six years old are freely available through the BHL. All URLs and DOIs also are made active in the online version of each article, by inserting an embedded hyperlink taking the online reader directly to the related publication or website.

The other new initiatives recognized historic field naturalists and awarded current publications. Beginning in issue 3 and as part of Canada's 150th birthday celebration in 2017, a section was added to the News and Comments to formally recognize Canada's greatest field naturalists. The first two Greatest Canadian Field-Naturalists were James Fletcher and John Macoun. A new award for the best paper published in the current volume of *The Canadian Field-Naturalist*, the James Fletcher Award, also was established in the same issue

Table 1. The 2017 (2016) circulation of *The Canadian Field-Naturalist*. Compiled by Eleanor Zurbrigg from the subscription list for 131(4).

Subscriber Type	Canada	USA	Other	Total
OFNC Members	51 (58)	4 (3)	0 (1)	55 (62)
Subscriptions:				
Individual	26 (21)	7 (6)	0 (1)	33 (28)
Institutional	73 (84)	106 (116)	12 (13)	191 (213)
Total	150 (163)	117 (125)	12 (15)	279 (303)

TABLE 4. Number of pages per section published in *The Canadian Field-Naturalist*, volume 131 (130), by issue.

	Issue				
	1	2	3	4	Total
Editorials/Editors' Report	0 (0)	0 (3)	2 (0)	1 (0)	3 (3)
Articles	67 (63)	47 (73)	47 (43)	42 (59)	203 (238)
Notes	7 (18)	17 (14)	30 (14)	27 (21)	81 (67)
Thematic Collections	5 (–)	8 (–)	0 (–)	0 (–)	13 (–)
Tributes	0 (0)	0 (0)	0 (0)	0 (18)	0 (18)
Book Reviews*	14 (8)	15 (4)	15 (9)	13 (11)	57 (32)
News and Comment†	2 (1)	1 (2)	6† (3)	12 (4)	21 (10)
Reports‡	19 (0)	0 (4)	0 (15)	0 (0)	19 (19)
Erratum	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Index	– (–)	– (–)	– (–)	9 (7)	9 (7)
Total	114 (90)	88 (100)	100 (84)	104 (120)	406 (394)

*Includes reviews and new titles.

†Includes Greatest Canadian Field-naturalists and announcement of James Fletcher Award.

‡Includes Annual Business Meeting Minutes, Annual Committee Reports, Financial Statements, and Awards.

of volume 131; all these are available at https://doi.org/10.22621/cfn.v131i3.2071.

Fifty-seven manuscripts were submitted to *The Canadian Field-Naturalist* in 2017, 12 fewer than in 2016; all were submitted using the Online Journal System, some after an initial email submission. Ten of the 59 were for a Special Issue, "Studies on Canadian Amphibians and Reptiles in Honour of Dr. Francis Cook", scheduled for publication in 2018; one of those submitted in 2017 for the Special Issue was withdrawn because the author had insufficient time for revision and another did not make the revision deadline for the Special Issue. Only six of the 57 submitted manuscripts were not accepted for publication upon initial submission or review and one was withdrawn meaning 89.5% were accepted or undergoing revision. In 2016, 82.6% of the 69 submissions were accepted for publication and either published or undergoing further revision and review. A total of 24 articles, 21 notes, and two thematic collections were published in 2017 (Table 2).

Dwayne Lepitzki was *Editor-in-Chief* for volume 131 while Amanda Martin, the *Assistant Editor*, edited content, proofread galleys, and sent and received author order and transfer of copyright forms. Sandra Garland and John Wilmshurst proof-read and copy-edited manuscripts. Wendy Cotie typeset galleys, provided corrections for page proofs, and created pdfs. Barry Cottam requested books for review, selected reviewers, edited submitted reviews, and prepared the new titles listings. Ken Young continued with the tasks of managing subscriptions, page charge invoices, and budget tracking although Eleanor Zurbrigg assumed the duties of managing subscriptions in the summer of 2017. William Halliday, Online Journal Manager and Webmaster, provided digital content to subscribers, posted tables of contents, abstracts, and pdfs on *The Canadian Field-Naturalist* website, and prepared the Index. Our Associate Editors managed manuscripts, provided reviews and recommendations, and guided authors through the revision process. The Publication Committee, chaired by Jeff Saarela and consisting of Annie Bélair, Dan Brunton, Carolyn Callaghan, Paul Catling, Barry Cottam, William Halliday, Diane Kitching, Dwayne Lepitzki, Amanda Martin, Karen McLachlan Hamilton, Frank Pope, David Seburn, and Eleanor Zurbrigg effectively guided the operation of the journal. We are indebted to our very dedicated team.

The following Associate Editors managed, assessed, and reviewed manuscripts published in volume 131: R. Brooks, University of Guelph, emeritus, Guelph ON (1 manuscript); P.M. Catling, Agriculture and Agri-Food Canada, retired, Ottawa ON (2); F. Chapleau, University of Ottawa, Ottawa ON (2); F.R. Cook, Canadian Museum of Nature, Emeritus, Ottawa ON (2); J. Foote, Algoma University, Sault Ste. Marie ON (8); G. Forbes, University of New Brunswick, Fredericton NB (3); A.J. Gaston, Environment Canada, Emeritus, Ottawa ON (2); W. Halliday, University of Victoria, Victoria, BC (2); T. Jung, Yukon Government, Whitehouse YT (5); D. Lepitzki, Banff AB (1); D.F. McAlpine, New Brunswick Museum, Saint John NB (7); J. McCraken, Bird Studies Canada, Port Rowan, ON (3); G. Mowat, government of British Columbia, Nelson BC (1); D.W. Nagorsen, Mammalia Biological Consulting, Victoria BC (1); M. Obbard, Ontario Ministry of Natural Resources and Forestry, Peterborough ON (1); J.M. Saarela, Canadian Museum of Nature, Ottawa ON (3); J. Skevington, Agriculture and Agri-Food Canada, Ottawa ON (1).

The following referees reviewed manuscripts published in volume 131 (number of manuscripts reviewed >1 in parentheses): Steve Ackers, Oregon State University; Kathryn Aitken, Yukon College (2); Noel Alfonso, Canadian Museum of Nature; Robert Alvo, Ottawa ON (2); Yves Aubrey, Environnement et Changement Climatique Canada; Shannon Barber-Meyer, US Geological Survey; Jason Beason, The Bird Conservancy; Rene

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Book Reviews

News and Comment

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