

Overwintering site fidelity and communal hibernation predispose Northern Map Turtles to mass mortality events

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Abstract

Mass mortality events appear to be increasing in intensity and frequency, so understanding their causes and consequences is imperative for wildlife conservation. We report on a mass mortality event in a population of Northern Map Turtles (*Graptemys geographica* (LeSueur, 1817)). At a communal overwintering site, 142 carcasses (ca. 10% of population) were recovered, seemingly depredated by river otters (*Lontra canadensis* (Schreber, 1777)). We compared the size and sex of the carcasses to those of turtles that survived. Smaller turtles and males were more likely to be depredated than larger turtles and females. Using captures made at the same overwintering site between 2003 and 2022, we assessed the vulnerability of this population to mass mortality events during winter. Nearly 60% of the 1875 turtles marked between 2003 and 2022 used the overwintering site where the mass mortality event occurred at least once. On average, turtles overwintered at the site at least 38% of the winters between their first and last capture. Our study shows how behaviour and physiology interact to predispose a species to mass mortality events and ecological traps. Protecting overwintering sites and minimizing human pressures affecting winter depredation may be essential for the preservation of certain turtle populations.

Key words: Northern Map Turtle, Graptemys geographica (LeSueur, 1817), predation, mass mortality events, site fidelity, overwintering

Introduction

Die-offs, also known as mass mortality events, have been reported in a wide range of animal taxa from around the globe (Reed et al. 2003; Fey et al. 2015). These events, broadly defined as sudden and marked increases in mortality rates, can push populations towards extinction (Lande 1993). Mass mortality events are especially concerning for long-lived species with slow life histories, as it may take decades for populations of such species to recover from the loss of only a few adults (Brooks et al. 1991; Keevil et al. 2018). Mass mortality events appear to be increasing in frequency and amplitude, and nearly 20% of them are caused by human actions (Fey et al. 2015). Mass mortality events are thus of particular interest to conservation scientists and wildlife managers (La and Cooke 2011; Ameca Y Juárez et al. 2012; Gasbarrini et al. 2021), but documenting them is challenging because such events remain relatively rare and are unpredictable (Reed et al. 2003).

Mass mortality events have various causes. Among biotic interactions (excluding those with humans), diseases and biotoxicity account for large (26.3% and 15.8%, respectively) proportions of mass mortality events (Fey et al. 2015). Predation, on the other hand, appears to be a rare cause of mass mortality events (Young 1994). Severe predation events can nonetheless have dramatic and long-lasting demographic consequences on populations (Festa-Bianchet et al. 2006; Keevil et al. 2018). Moreover, human activities can change predator abundance and behaviour and, by doing so, cause rapid predation-induced declines in prey populations (Williams et al. 2004; Ekroos et al. 2012). When predation risk increases rapidly, individuals may not be able to adjust through phenotypic plasticity or the populations may not have sufficient time to mount an adaptive response, hence creating ecological or evolutionary traps (Kokko and Sutherland 2001; Battin 2004; Hale and Swearer 2016).

Species with high site fidelity have been argued to be predisposed to fall into ecological traps (Merkle et al. 2022). Animals often return to sites they have previously used for reproduction, foraging, migration, and overwintering. Such site fidelity can be adaptive in both predictable and unpredictable environments (Switzer 1993), but human-induced rapid environmental changes (Sih et al. 2016) can render site fidelity maladaptive (Merkle et al. 2022). Indeed, site fidelity can be viewed as a form of behavioural rigidity, and faithful individuals may lack the flexibility to seek alternative sites when previously used sites become ecological sinks due to rapid environmental changes, such as changes in predation pressure (Ekroos et al. 2012).

Fidelity to overwintering sites as well as communal hibernation have been reported in several freshwater turtles in cold climates (Brown and Brooks 1994; Litzgus et al. 1999; Graham et al. 2000; Ultsch et al. 2000; Galois et al. 2002; Newton and Herman 2009). These behaviours may be adaptations to minimize winter predation risk as winter predation on turtles can be substantial (Brooks et al. 1991; Lanszki et al. 2006). Overwintering freshwater turtles appear to be particularly vulnerable to predation because cold temperatures limit or prevent them from escaping predators or defending themselves against attacks given the depression in metabolic rates and constraints on locomotion induced by cold. Turtles may thus return to, and aggregate at overwintering sites that have been historically difficult or impossible to access by predators such as the river otter (Lontra canadensis (Schreber, 1777)) and the American mink (Neovison vison (Schreber, 1777)) that can hunt under the ice. Mass winter predation events of turtles may thus represent instances in which previously inaccessible overwintering sites became accessible to predators due to natural or human-induced environmental changes. Once overwintering sites are accessible to, and known to predators such as otters, overwintering turtles would become a predictable and easily obtained food source at a time when other prey are limited (Lanszki et al. 2006). Thus, turtles could experience very high predation rates.

Documenting rare mass mortality events is the first step in understanding their causes and consequences (Catrysse et. al. 2015; Stacy et al. 2014; Gasbarrini et al. 2021). Moreover, assessing the behavioural predispositions of populations to mass mortality events and ecological traps may help minimize their occurrence and impacts (Merkle et al. 2022). Doing so is particularly important for the conservation of local turtle populations. Turtles are globally at risk (Stanford et al. 2020). The reasons for their decline are varied, but the slow life history of turtles greatly limits their ability to recover from sudden increases in adult mortality (Congdon et al. 1993, 1994), including those caused by mass predation events (Keevil et al. 2018).

Here, we report on a mass winter predation event in a population of Northern Map Turtles (Graptemys geographica (Lesueur, 1817)) in Opinicon Lake, Ontario, Canada. In April 2022, we recovered 142 turtle carcasses at an overwintering site we had been monitoring for 19 years. We first describe the size and sex of the depredated turtles as well as the type of trauma inflicted. Because the population had been the focus of a mark-recapture study since 2003, we also have a unique opportunity to test the effect of size on the probability of being preved upon. This is important because the population consequences of mass mortality events will be especially severe if large turtles and if females are more susceptible to predation. Finally, we use our long-term mark-recapture data to assess the vulnerability of overwintering map turtles to mass mortality events by estimating overwintering site fidelity. Our findings will be of interest to wildlife managers and stakeholders engaged in turtle conservation and to population biologists more generally.

Materials and methods

Study site

We conducted this study at the Queen's University Biological Station, approximately 100 km south of Ottawa, Ontario, Canada. We captured map turtles in Opinicon Lake, a small (7.9 km²) and shallow (mean depth = 2.5 m; maximum depth = 10.7 m) mesotrophic lake that is part of the Rideau Canal World Heritage Site, between 2003 and 2022. We captured turtles annually, typically while snorkeling in the vicinity of overwintering sites, basking sites, and nesting sites. Turtles were individually marked by drilling or notching their marginal scutes in unique combinations (2003– 2021) or with passive integrated transponders (2022) inserted in the body cavity. The focal overwintering site of this study is a 0.16 km² island. Our field observations as well as eDNA surveys (Feng et al. 2019) suggest that there are two main clusters of overwintering turtles around the island.

Mass mortality event

On 21 April 2022, 12 days after the ice cover on the lake melted, 142 Northern Map Turtle carcasses were recovered while snorkeling at one of two main overwintering clusters. The carcasses were all recovered along an approximately 50 m stretch of shoreline in water less than 2 m deep. Many of the carcasses were in heaps of several individuals (Fig. 1a). All the carcasses had clear signs of depredation, such as crushed shells and missing appendages (Figs. 1a and 1b). We determined the sex of the dead turtles from the shape of their shells (at equal size, male map turtles are more oblong than females), recorded missing appendages (limbs, head, and tail), and whether each shell was intact. On intact shells, we measured carapace length (CL) and carapace width (CW) using forestry calipers (0.5 mm accuracy). Straight CL is the most reported size measurement for freshwater turtles, but it could not be measured in 64 individuals due to extensive shell damage. In these cases, we estimated CL from CW using equations derived from our study population. To derive these equations, we used measurements from live turtles (392 females, 720 males, and 609 individuals too small to be sexed) captured between 2003 and 2022. We only used turtles within the range of the CW of the dead turtles to derive the equations to predict CL from CW in millimetres,

Females: CL = -9.50 + 1.25 * CW (n = 392; $R^2 = 0.97$). Males: CL = -27.98 + 1.55 * CW (n = 720; $R^2 = 0.95$). Sex unknown: CL = -21.96 + 1.45 * CW (n = 609; $R^2 = 0.90$).

The vicinity of the area where the carcasses were recovered was snorkelled on three other occasions between 22 April and 1 May 2022, and no other carcasses were recovered, although an undetermined number of shells were seen in inaccessible crevices between boulders. On these three occasions, we captured 73 live turtles within 200 m of where the carcasses were recovered. Map turtles at our study site overwinter very close to one another (Fig. 1d) and disperse from their overwintering sites 2-3 weeks after the surface ice melt, which usually occurs in mid to late April. We can thus assume that the turtles we captured live overwintered nearby the turtles that were depredated and were thus presumably available to the predators. We tested whether size affected the probability of a turtle being depredated with a logistic regression with CL as the predictor variable and whether a turtle was encountered dead or alive as the binary response variable. Northern map turtles display extreme sexual size dimorphism with adult



Fig. 1. (*a*) A heap of dead Northern Map Turtles (*Graptemys geographica*) as recovered in Opinicon Lake, ON, Canada on 21 April 2022. (*b*) Example of a Northern Map Turtle carcass with shell damage. (*c*) Example of a Northern Map Turtle carcass with all limbs and tail severed. (*d*) Under the ice photograph of overwintering Northern Map Turtles in Opinicon Lake showing that turtles are exposed, and aggregated.



females reaching twice the CL of males (Vogt et al. 2018). The limited overlap in body size between the sexes confounds the effects of size and sex in statistical analyses. We thus performed logistic regressions separately for each sex. Because we were not able to confidently determine the sex of 25 individuals (19 dead and 6 live), we randomly assigned half of these individuals as males and the other half as females. Finally, we tested whether size affected the probability of the shell being crushed by the predators using a logistic regression with CL as the predictor variable and whether the shell was intact as the response variable.

Overwintering site fidelity

We estimated overwintering site fidelity with the following equation:

 $SF=N_w/N_p$

where N_w is the number of winters a turtle was known to have overwintered at the site and N_p is the possible number of winters that individual could have overwintered at the site and could have been captured in the spring. To calculate N_w for an individual, we counted the number of years that individual was captured anywhere around the perimeter of the overwintering island between the spring thaw and 14 May. We assumed that turtles captured between these dates had hibernated around the island. We calculated N_p by taking the difference between the last and first year an individual was captured. This value was then corrected to account for the number of years the overwintering site was not sampled in the spring (2003 and 2017) or during which limited (<25 captures) sampling took place (2016: n = 8; 2019: n = 25). For instance, if a turtle was captured for the first time in 2005 and for the last time in 2018, its N_p would be 11. We divided the data to form three fidelity horizons: short-term fidelity $(N_{\rm p}$ < 7), medium-term fidelity ($N_{\rm p}$ = 7–11), and long-term fidelity ($N_p = 12$ –17). These horizons represent three approximately equal bins based on the temporal extent of our data. We then tested the effects of the horizon and of sex on mean fidelity using a two-way analysis of variance (ANOVA). To further examine long-term site fidelity, we also determined the proportion of turtles that were captured at least once at the

Table 1. Results of logistic regression analysis with carapace length as the predictor and whether the shell was intact as the response variable for 142 Northern Map Turtle (*Graptemys geographica*) carcasses collected in Opinicon Lake, ON, Canada.

Predictor	Estimate (SE)	χ^2	df	р	\mathbb{R}^2
Intercept	- 16.07 (2.83)	32.24	1	<0.0001	
Carapace length (mm)	0.14 (0.02)	32.68	1	<0.0001	
Overall model					
Likelihood ratio test		61.22	1	<0.0001	0.31

Fig. 2. The relationship between carapace length and the probability of a dead turtle being recovered with an intact shell
based on carcass measurements from 142 depredated Northern Map Turtles (Graptemys geographica) recovered in April 2022 at
a communal overwintering site in Opinicon Lake, ON, Canada. Line shows logistic fit.



overwintering site in the first 4 years of the study (2004–2007) as well as at least once in the last 4 years of the study (2019–2022).

This research was approved by the Animal Care Committee at Carleton University (protocol No. 118468) and was conducted under an Ontario Ministry of Natural Resources wildlife scientific collector's authorization (No. 1097538).

Results

Mass mortality event

Of the 142 carcasses recovered, 105 were males, 18 were females, and we could not confidently determine the sex for 19 carcasses due to their small size or extensive damage. The carcasses ranged in CL from 77 to 158 mm. In the 10 days following the discovery of the carcasses, within 200 m of where the carcasses were recovered, we captured 32 females, 35 males, and 6 individuals too small for the sex to be confidently assigned. The turtles encountered alive ranged in CL from 52 to 271 mm. Thirty-six percent (18/50) of females were found dead, while 75% (105/140) of males and 76% (19/25) of unsexed individuals were found dead. The proportion of turtles found dead differed significantly between the three groups (likelihood ratio test: $\chi^2_{[2]} = 25.2$, p < 0.0001). Males were 5.3 times more likely (p < 0.0001) to be found dead

than females and unsexed turtles were 5.6 times more likely (p = 0.0018) to be found dead than females. Males and unsexed individuals were as likely to be found dead as alive (p = 0.91).

Seventy-nine carcasses had a broken shell. All turtles with broken shells missed all their appendages and viscera. Among the carcasses with intact shells, 70% were missing all limbs, their tail, and head, while 30% still had their head, but were missing their tail and limbs. Only one carcass was missing its hind limbs and tail. The logistic regression showed that the probability of the shell being crushed decreased significantly with CL (Table 1; Fig. 2). Each 1 mm increase in CL increased the probability of the shell being intact by 15%. The logistic model correctly classified 79% of the broken shell, and 77% of the intact shells based on CL, using a probability of 0.5 as the cut-off between the two states (broken or unbroken).

In males (n = 152), CL was not a significant predictor of the probability of being found alive or dead in the spring (likelihood ratio test: $\chi^2_{[1]} = 0.94$, p = 0.33; Fig. 3A). In females (n = 63), however, the probability of being found alive increased significantly with CL (Table 2; Fig. 3B). Over the entire range of CL in the sample (52–271 mm), the odds ratio of being found alive versus dead was 55. Each 1 mm increase in CL increased the probability of a female being encountered alive 1.8%. The logistic model correctly classified 67% of the **Fig. 3.** The relationship between carapace length and the probability of a (A) male or (B) female Northern Map Turtle (*Graptemys geographica*) being encountered alive at a communal overwintering site in April 2022, in Opinicon Lake, ON, Canada. Lines show logistic fit.



Table 2. Results of logistic regression analysis with carapace length as the predictor and whether a turtle was recovered alive for 63 female Northern Map Turtles (*Graptemys geographica*) collected in Opinicon Lake , ON, Canada.

Estimate (SE)	χ^2	df	р	R ²
- 2.01 (0.86)	5.52	1	0.018	
0.018 (0.007)	6.89	1	0.009	
	10.00	1	0.002	0.12
	Estimate (SE) - 2.01 (0.86) 0.018 (0.007)	Estimate (SE) χ² -2.01 (0.86) 5.52 0.018 (0.007) 6.89 10.00	Estimate (SE) χ² df -2.01 (0.86) 5.52 1 0.018 (0.007) 6.89 1 10.00	Estimate (SE) χ² df p -2.01 (0.86) 5.52 1 0.018 0.018 (0.007) 6.89 1 0.009 10.00 1 0.002

dead females, and 54% of the live females based on CL, using a probability of 0.5 as the cut-off between the two states (dead or alive). The largest female found dead had a CL of 158 mm. Forty percent of the females found alive had a CL > 158 mm.

Overwintering site fidelity

Between 2003 and 2022, we individually marked 1875 northern map turtles in Opinicon Lake and 1108 (59%) were captured at least once in the vicinity of the communal overwintering site before 14 May and are thus assumed to have overwintered there. Of those, 612 turtles were females, 471 were males, and 25 were too small for sex to be determined based on external characteristics. We used data from 662 turtles that were captured at least once at the overwintering site and at least on two different years to calculate mean fidelity. Overall, fidelity ranged from 6% to 100% with a mean of 38%. Site fidelity did not differ between males and females ($F_{[1,656]} = 2.57$; p = 0.11, $R^2 = 0.003$) and there were no interactions between fidelity horizon and sex ($F_{[2,656]}$ = 0.31, p = 0.74, $R^2 = 0.0006$). The fidelity horizon, however, had a significant effect on site fidelity ($F_{[2,656]} = 169.54$, p < 0.0001, $R^2 = 0.34$). A post-hoc Tukey's HSD test comparing the means between fidelity horizons revealed that short-term fidelity was significantly higher than both medium-term and long-term fidelity, which did not differ from one another (Fig. 4).

We captured 345 individuals (167 females, 176 males, and 2 individuals too small for sex to be determined based on external characteristics) at the overwinter site before 14 May between 2004 and 2007, 120 of which were known to be alive between 2019 and 2022. Of these 120 turtles, 104 (87%) were recaptured at least once at the overwintering site between 2019 and 2022. **Fig. 4.** Mean overwintering site fidelity of Northern Map Turtle (*Graptemys geographica*) from Opinicon Lake, ON, Canada based on long-term (12–17 years), medium-term (7–11 years), and short-term (less than 7 years) fidelity horizons. Error bars show 95% confidence interval. Similar letters indicate there are no differences in mean fidelity for the respective fidelity horizons based on one-way analysis of variance, while differing letters indicate significant differences.



Discussion

The identity of the predators responsible for the mass mortality event that we reported here is unknown, but only two species in our study area are capable of preying upon turtles overwintering under the ice: the American mink and the river otter. The river otter has been documented to cause mass mortality events in turtles, including during winter (Brooks et al. 1991; Stacy et al. 2014), but we are not aware of mass mortality event caused by the American mink. Adult female Northern Map Turtles at our study site can reach 298 mm in CL, yet only turtles under 158 mm were preyed upon and only the smallest turtles were crushed. Large females were most likely available to the predators because Northern Map Turtles overwinter in dense groups of individuals of various sizes at our study site (see below). The river otter is certainly capable of preying on turtles as large or larger than adult female Northern Map Turtles (Brooks et al. 1991; Stacy et al. 2014). The American mink is about eight times lighter than the river otter, and its estimated bite force is 3.8-4.5 times weaker (Christiansen and Wroe 2007; Harstone-Rose et al. 2019). The pattern in probability of predation in relation to size may thus reflect prey size limitation by the smaller American mink, or size selectivity by the larger river otter. The fact that many shells were crushed suggests, however, that otters were responsible for the mass mortality event. Magwene and Socha (2013) measured the load required to break the shell of red-eared sliders similar in size to Northern Map Turtles. The point load (mimicking a pressure from a tooth) required to break the smallest shells was approximately 400 N. The maximum estimated bite force of American mink is 58 N compared to 220 N for river otter (Chirstiansen and Wroe 2007). The estimated bite force of the river otter is thus much closer to the breaking point of turtle shells under a point load than that of the American mink.

If otters are indeed responsible for the mass mortality event, they appear to have discriminated against larger turtles that happen to be adult females due to the extreme sexual size dimorphism in this species. Size selectivity may be related to the handling cost of turtles of different sizes. Small turtles can be crushed, while larger turtles must be dismembered as indicated by the significant relationship between CL and the probability of being crushed. Larger turtles, such as adult females, are presumably harder to handle and dismember than smaller ones. Thus, when turtles of all sizes are available, otters may favour smaller ones. Targeting smaller turtles would increase foraging efficiency as less time would be spent handling and dismembering turtles. This may be important if overwintering turtles can respond to the presence of a predator. Albeit slow, Northern Map Turtles remain active under the ice in winter (Robichaud et al. 2023), so it may be possible for turtles to move away when a predator is detected. If this is indeed the case, reducing prey handling time would allow otters to make more dives before turtles in an area move to another area less accessible to otters.

The mass mortality event we documented here affected 9.4% of the estimated population of Northern Map Turtles in Opinicon Lake (Bulté et al. 2010). The overwintering behaviour and physiology of Northern Map Turtles appear to predispose them to mass mortality events. Communal overwintering is common in freshwater turtles in cold climates (Litzgus et al. 1999; Graham et al. 2000; Galois et al. 2002; Newton and Herman 2009; Pittman and Dorcas 2009), but Northern Map Turtles appear to form much larger overwintering aggregations than other turtles studied to date. Graham and Graham (1992) observed over 100 Northern Map Turtles overwintering at one location in the Lamoille River in Vermont, USA. In Opinicon Lake, the maximum number of Northern Map Turtles captured at the overwintering site in

one spring was 249, which represents 17% of the estimated population size (Bulté et al. 2010). Overwintering site fidelity of Northern Map Turtles in Opinicon Lake was relatively high, even in our longest term horizon (12-17 years), with the average turtle being detected at the overwintering site nearly once every 4 years (22% of the years). Our measure of overwintering site fidelity is certainly an underestimation given that we cannot capture all the turtles at the overwintering site every year. Some turtles disperse from the overwintering site within days of the spring thaw (G. Bulté, pers. obs.) and are thus not captured every year. In some years, sampling started 3-4 weeks after the spring thaw and thus after many individuals had already dispersed from the overwintering site. The observation that 86% of the turtles captured at the overwintering site between 2004 and 2007 and that were known to be alive between 2019 and 2022 were recaptured at the same overwintering site during that latter period demonstrates that many turtles in a population are faithful to their overwintering sites for more than a decade.

Physiological constraints and predation risk may be the main factors dictating where Northern Map Turtles can safely overwinter, and thus the reasons for their gregarious and faithful overwintering habits. Northern Map Turtles are anoxia intolerant, so they must seek overwintering sites with enough dissolved oxygen to sustain their aerobic metabolism over the winter (Reese et al. 2001). Such sites may be especially limited in lakes that are more likely to experience hypoxia and anoxia during winter than running waters. Northern Map Turtles seemingly meet their oxygen demand through cutaneous respiration in winter (Maginniss et al. 2004), so they must remain fully exposed to allow the flow of water over their skin (Crocker et al. 2000; Robichaud et al. 2023). Moreover, at least in Opinicon Lake, Northern Map Turtles overwinter in shallow areas close to shore where the water is coldest, presumably to depress metabolism and minimize oxygen demand (Robichaud et al. 2023). Finally, Northern Map Turtles can overwinter at high density with individuals sometimes touching each other (Graham and Graham 1992; Robichaud et al. 2023). This behaviour may be a form of selfish herd to minimize individual predation risk. But regardless of why they aggregate, the high density of exposed turtles in shallow areas close to shore predisposes overwintering Northern Map Turtles to mass predation events in winter.

Suitable overwintering sites appear limited, at least at out study site. In a radio-telemetry study of 53 Northern Map Turtles conducted between 2004 and 2007 in Opinicon Lake, Bulté et al. (2008) located only one other overwintering site, but that additional site was in a neighbouring lake. A single adult female travelled on land in fall to reach that lake and returned to Opinicon Lake in spring. More recently, Feng et al. (2019) used eDNA and remotely operated vehicle surveys to locate overwintering sites and were able to confirm only one additional overwintering site in Opinicon Lake, but only a single turtle was observed under the ice at that site. Thus, after nearly 20 years of studying this population with various techniques, we have located only one additional overwintering site in Opinicon Lake, and this site appears to be attended by very few turtles. Other overwintering sites may exist in Lake Opinicon, but they are certainly not used by as

many turtles as the focal site of this study. The fact that overwintering Northern Map Turtles aggregate in other areas (reviewed by Vogt et al. 2018) suggests that suitable overwintering sites are generally uncommon. Identifying and protecting such sites from human encroachments may thus be essential for the local persistence of Northern Map Turtle populations.

The mortality documented here, combined with knowledge of overwintering behaviour (e.g., aggregation and fidelity) and physiology, shows that populations of Northern Map Turtles are predisposed to mass mortality events and vulnerable to fidelity-induced ecological traps. Human activities reducing oxygen availability or increasing predation risk by interfering with ice formation are particularly concerning for overwintering turtles. De-icing propellers (a.k.a. bubblers) may be problematic in some areas. These devices are used to agitate the surface of the water to prevent ice formation around docks and boathouses and can thus create entry points for otters and minks in the winter. De-icing propellers are now common in Opinicon Lake (21 were observed in winter 2021-2022) and in neighbouring lakes, and may turn some overwintering sites into ecological traps by providing entry points for predators. Studies examining the effects of de-icing propellers (or other activities or habitat alterations that may alter predator access) on winter foraging by minks and otters will offer important insights into their potential effects on overwintering turtles. Changes in ice phenology due to global warming (Huang et al. 2022) may also increase predation risk at communal overwintering sites. While little can be done locally to prevent climate change from happening, identifying and protecting as many communal overwintering sites as possible will help populations persist.

Acknowledgements

We thank the staff of the Queen's University Biology Station as well as S. Dollin for assisting with data collection. This study was funded by the Natural Sciences and Engineering Research Council of Canada, Parks Canada, Carleton University, and University of Ottawa through grants to GBD, GB, SJC, and JAR.

Article information

History dates Received: 4 July 2023 Accepted: 15 August 2023 Version of record online: 30 October 2023

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Data availability

The data are not publicly available but can be shared upon request by contacting Grégory Bulté at gregory.bulte@carleton.ca.

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Competing interests

The authors do not have any competing interests.

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