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Burying in lake sediments: A potential tactic used by female northern map turtles to avoid male harassment

Grégory Bulté[1] | **Jessica A. Robichaud**[1] | **Steven J. Cooke**[1] | **Heath A. MacMillan**[1] | **Gabriel Blouin-Demers**[2]

[1]Department of Biology, Carleton University, Ottawa, Ontario, Canada

[2]Department of Biology, University of Ottawa, Ottawa, Ontario, Canada

Correspondence
Grégory Bulté, Department of Biology, Carleton University, 1125 Colonel by Drive, Ottawa, Ontario, K1S 5B6, Canada.
Email: gregory.bulte@carleton.ca

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Abstract

How often males and females need to mate to maximize their fitness is a source of sexual conflict in animals. Sexual conflict over mating frequency can lead to antagonistic coevolution in which males employ tactics to coerce females into mating, while females resist or evade mating attempts by males. Here, we report on a novel burying behavior observed in female northern map turtles (*Graptemys geographica*) in Opinicon Lake, Ontario, Canada that appears to function as a tactic to avoid male detection during the mating season. Underwater videos indicated that females are heavily solicited during the mating season with over half the females being actively pursued by males. Biologgers indicated that females are less active and remain deeper than males during the mating season. Our data strongly suggest that female northern map turtles avoid intense solicitation and potential harassment by males by burying themselves in lake sediments. This behavior appears to be a low-cost solution for females to reduce the costs of resistance and mating while they are constrained to habitats with high male densities for overwintering.

KEYWORDS
harassment, mating, sexual conflict

1 | INTRODUCTION

How often male and female animals need to mate to maximize their fitness is a source of sexual conflict (Arnqvist & Nilsson, 2000; Parker, 2006). This conflict is rooted in the difference in reproductive allocation between the sexes (Parker, 2006; Trivers, 1972). When males solely contribute sperm to the production of offspring, their fitness is primarily limited by the number of females with which they can mate. Females, in contrast, invest more resources than males in the production of offspring so their fitness is limited more by resource availability than by mating opportunities. The fitness of females thus tends to be optimized at a lower mating frequency than the fitness of males. Therefore, males generally seek to mate more frequently than females (Parker, 2006; Trivers, 1972). In fact, females may even experience decreased fitness if they mate as frequently as males because mating involves costs in the form of time, energy, injuries, disease transmission, and exposure to predators (Daly, 1978). This sexual conflict over mating frequency can lead to antagonistic coevolution in which males employ tactics to coerce females into mating, while females resist or evade mating attempts by males (Clutton-Brock & Parker, 1995; Rowe et al., 1994).

Male coercive mating tactics include forced copulation, punishment, and harassment (Clutton-Brock & Parker, 1995). The goal of harassment and intimidation by males is to elevate the cost of female resistance above the cost of mating so that females mate to minimize this cost (Rowe et al., 1994). In many species, females may mitigate the cost of resistance by avoiding male detection rather than by physically resisting mating attempts. Female tactics used to avoid male detection are diverse and include hiding (Krupa et al., 1990; Pineaux & Turgeon, 2016), male mimicry (Cook et al., 1994; Falk et al., 2021; Galán & Price, 2000; Gosden & Svensson, 2009), concealing visual cues (Ide, 2011), semiochemical crypsis (Fischer et al., 2018), dispersing from habitats with high male density (Shine et al., 2005), and even feigning death (Dittrich & Rödel, 2023; Khelifa, 2017).

Here, we report on a novel behavior observed in female northern map turtles (*Graptemys geographica*) that appears to function as a tactic to avoid male detection during the mating season. In October 2020, we observed several female northern map turtles buried in loose sediments while we were snorkeling near a communal overwintering site in Opinicon Lake (Ontario, Canada). We documented this behavior on 27–28 October 2023 by surveying the lake bottom with an underwater remotely operated vehicle (ROV: Open ROV, Trident, San Francisco, USA). During these 2 days, we observed 32 turtles: 29 adult females, one adult male, one immature female, and one turtle we could not sex because it was too far in the field of view. Turtles could easily be sexed from the ROV recordings due to the pronounced sexual dimorphism in body size, head size, tail length, and body shape in northern map turtles (Vogt et al., 2018). Of the 29 adult females observed, three (10%) were moving along the bottom and 26 (90%) were immobile on the bottom. Of the 26 immobile females, 15 (58%) were fully exposed, five (19%) had approximately half of their body buried in the sediments, and nine (35%) were completely buried with only their heads out of the sediments (Figure 1). We believe the burying behavior is unrelated to overwintering because it was observed at relatively high water temperatures (12–16°C) and nearly 2 months before the lake surface froze. Moreover, northern map turtles at our study site overwinter fully exposed, at a mean depth of 1.5 m, on a rocky substrate (Robichaud et al., 2023). Lake sediments are anoxic and remaining exposed is presumably essential for overwintering northern map turtles to maintain cutaneous gas exchange (Reese et al., 2001). Finally, burying was observed only in adult females, suggesting a sex-specific function. We therefore hypothesize that burying is used by adult females to conceal themselves from males, which reduces the costs of harassment and mating.

To test this hypothesis, we re-analyzed data collected in two previous studies on the same turtle population. Firstly, we re-analyzed footage from a mate choice experiment conducted in the field (Bulté et al., 2021) to quantify the intensity of solicitation by males (and thus potential harassment) of active females during

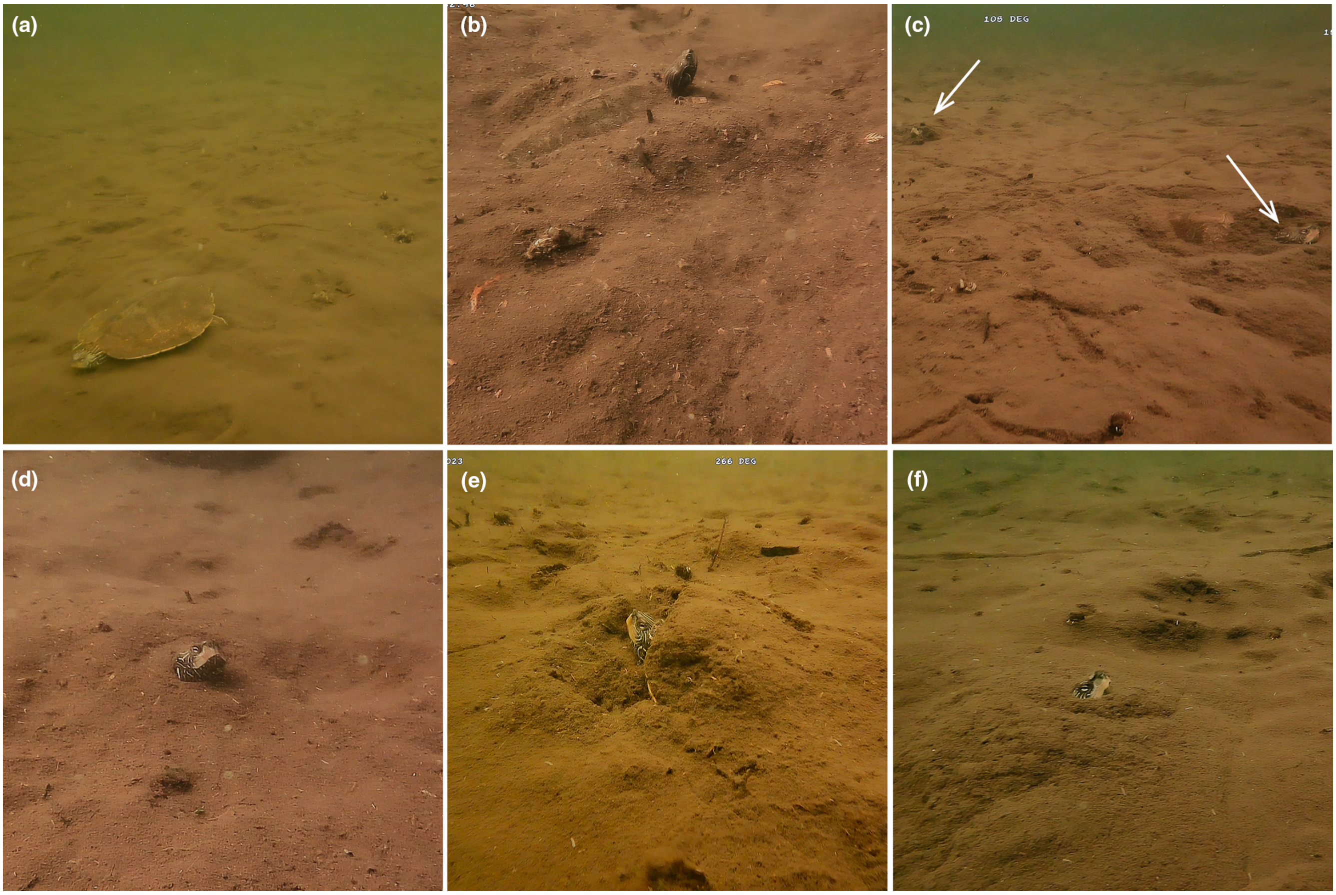

FIGURE 1 Examples of female northern map turtles observed with a remotely operated vehicle on 26–27 October 2023 in Opincon Lake, Ontario, Canada. (a) Exposed female. (b) Partly buried female. (c–f) Fully buried females.

the mating season. If male solicitation is infrequent, the burying behavior likely serves another function than male avoidance. Secondly, we re-analyzed biologging data collected at the same location and time of the year during which the burying behavior was observed (Robichaud et al., 2023) to test for differences in depth and locomotor activity between the sexes. If the burying behavior is used by females to avoid male detection, females should on average be less active and remain at a more constant depth than males.

2 | MATERIALS AND METHODS

2.1 | Study system

Our study took place in Opinicon Lake in eastern Ontario, Canada. The population of northern map turtles in this lake has been monitored through mark recapture since 2003 and has been the focus of several studies on reproductive biology (Bulté et al., 2008, 2013; Banger et al., 2013; Bulté et al., 2018; Bulté et al., 2021; Bulté & Blouin-Demers, n.d.). The estimated population size in Opinicon Lake is around 1500 individuals and the adult sex ratio is even (Bulté & Blouin-Demers, 2009). Most turtles in this study population overwinter around a single island (Bulté et al., 2023). Northern map turtles in Opinicon Lake mate when they are aggregated at the communal hibernacula (Bulté et al., 2018, 2021). Mating attempts and males pursuing females are regularly observed when snorkeling at the hibernacula both in late fall (October–November) and early spring (April–May). At the hibernacula, males seemingly compete for access to females in scrambles as they do not display aggressive behaviors towards each other (Bulté et al., 2021).

2.2 | Intensity of female solicitation by males during the mating season

In a previous experiment (Bulté et al., 2021), we used action cameras to record the response of free-ranging males to female decoys deployed at communal overwintering sites during the mating season. The female decoys received on average 5.4 male visits per hour, suggesting intense solicitation. This measure may not accurately reflect solicitation intensity, however, because the decoys might not replicate the exact cues used by males to detect and select females. During the experiment, adult females regularly moved through the field of view of the camera filming the decoys. We used these opportunistic observations to assess solicitation intensity as the proportion of females being pursued by at least one male as they moved through the field of view. To be considered a pursuit, the male (or males) had to be following the females immediately or swimming directly on top of them (Figure 2). We analyzed the recordings from 20 camera deployments over a 10-day period between 14 and 28 April 2017. The cameras recorded for approximately 7 h per day and were deployed between 0700 h and 0800 h (177 h of video in total).

2.3 | Locomotor activity and depth during the mating season

We quantified locomotor activity using biologging data collected as part of a previous study on overwintering behavior (Robichaud et al., 2023). Between 16 and 21 October 2020, we captured 17 adult females and 14 adult males by snorkeling at the communal overwintering site where the burying behavior was observed. We equipped each turtle with a biologger (22 × 45 × 8 mm, 11 g in air; Axy-5, TechnoSmArt, Guidonia Monticello, Italy) and a radio-transmitter (15 × 8.2mm, 1.5 g in air; NanoTag, Lotek, Newmarket, Ontario, Canada) to enable the recapture of the turtles and retrieval of the biologgers. We affixed the loggers and transmitters with epoxy to the posterior edge of the carapace. The loggers recorded acceleration (i.e., a proxy for locomotor activity), water temperature (±0.1°C), and depth (±5 cm) between 0700 h and 1700 h and between 2000 h and 2400 h. Acceleration was measured at a sample rate of 10 Hz with an 8-bit resolution and depth and temperature were recorded every second. All turtles were released by 22 October and the loggers started recording on 24 October. Due to transmitter and logger failures, we obtained data for 12 adult females (209–250 mm maximum carapace length) and 11 adult males (126–141 mm maximum carapace length). We calculated locomotor activity as the Overall Dynamic Body Acceleration (ODBA) following Shepard et al. (2008) and Brownscombe et al. (2018).

We tested for differences in behaviors between sexes using linear mixed effects linear models. We used mean daily depth, total daily ODBA per turtle, or temperature as the response variables and turtle sex as the predictor variable. In each model, turtle identity was included as a random effect to account for multiple measurements per individual and date as a covariate. We included an interaction between sex and date. We used the data for the period between the first day of recording (24 October) and the day before the ice formed on the lake (18 December).

This research was approved by the Carleton University Animal Care Committee (protocol # 10267) and conducted with a permit from the Ontario Ministry of Natural Resources and Forestry (permit #1085909).

3 | RESULTS

3.1 | Female solicitation by males during the mating season

During the field recordings, 140 adult females moved through the camera field of view. In total, 62 (44.3%) were not being pursued by males and 78 (56.7%) were pursued by at least one male; 51 (36.4%) were pursued by a single male, 25 (18.9%) were pursued by two males, and two (1.4%) were pursued by three males.

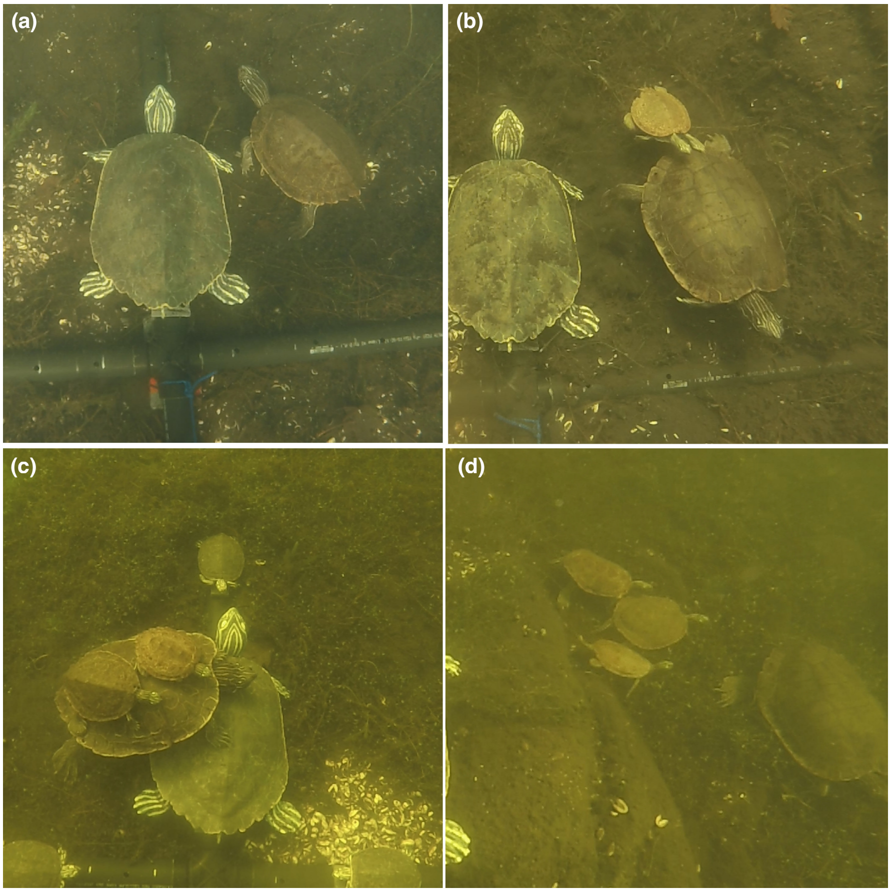

FIGURE 2 Examples of opportunistic observations of female northern map turtles during mate choice experiments in Opincon Lake, Ontario, Canada. (a) Female not pursued by males. (b) Female pursued by a single male. (c) Female pursued by two males. (d) Female pursued by three males.

3.2 | Activity patterns during the mating season

There was no effect of sex on temperature, but temperature declined through time (Table 1). The daily mean temperature for all the turtles steadily declined from 12.2°C to 1.1°C between 24 October and 18 December (Figure 3). Date and sex significantly affected ODBA and the interaction between these two variables was also significant (Table 1). The effect of sex on ODBA was most pronounced at the beginning of the measurement period (Figure 3) which corresponds to the period during which the burying behavior was documented (27–28 October). For instance, the ODBA of males was on average 34% higher than the ODBA of females during the first 7 days of sampling (24–31 October). In contrast, during the last 7 days of sampling (11–18 December), the ODBA of males was on average 8% higher than the ODBA of females. The effect of date on ODBA was more pronounced in males than in females (Figure 3). Only three of the 12 females showed significant relationships between date and ODBA ($p < .05$, $r = 0.26–0.37$). In contrast, the relationships between date and ODBA for the 11 males were all significant ($p < .001$) and stronger ($r = 0.58–0.80$). Between 24 October and 18 December, the mean ODBA of males declined by 38% while the mean ODBA of females declined by only 9%.

Date and sex significantly affected depth, and the interaction between these two variables was also significant (Table 1). As was the case for ODBA, the difference in mean depth was more pronounced early in the sampling period (Figure 3). For instance, during the first 7 days of sampling (24–31 October) females were on average 37 cm deeper than males, but only 7 cm deeper in the last 7 days of sampling (11–18 December). On average, females

TABLE 1 Summary statistics for the linear mixed effects models testing for sexual differences in behavior in northern map turtles from Opinicon Lake, Ontario, Canada from 24 October until 18 December 2020.

Variable	Estimate	SE	*t*-value	*p*-value
Overall dynamic body acceleration ($R^2 = 0.54$)				
Intercept	758.8	7.4	102.0	<.001
Sex	−56.8	6.1	−9.3	<.001
Date	−3.5	0.15	−23.5	<.001
Sex*Date	2.6	0.15	17.35	<.001
Temperature ($R^2 = 0.91$)				
Intercept	11.0	0.08	142.4	<.001
Sex	0.05	0.06	0.77	.45
Date	−0.18	0.001	−109.7	<.001
Sex*Date	−0.001	0.001	−0.80	.42
Depth ($R^2 = 0.49$)				
Intercept	2.63	0.11	24.4	<.001
Sex	0.31	0.10	2.9	.008
Date	−0.003	0.001	−3.3	<.001
Sex*Date	−0.007	0.001	−6.9	<.001

were shallower with time while males were deeper (Figure 3). The effect of date on depth was highly variable within sexes, but was generally stronger in females. Half of the females showed significant negative relationships ($p<.05$; $r=0.32$–0.79) between date and depth, while the other half did not show significant relationships between date and depth. Five males showed significant positive relationships ($p<.05$; $r=0.30$–0.44) between date and depth. Three males showed a significant negative relationship ($p<.05$; $r=0.26$–0.35) between date and depth, and two males showed no association between depth and date. Overall, the sexual differences in depth were small, and so was the effect of date on depth for both sexes.

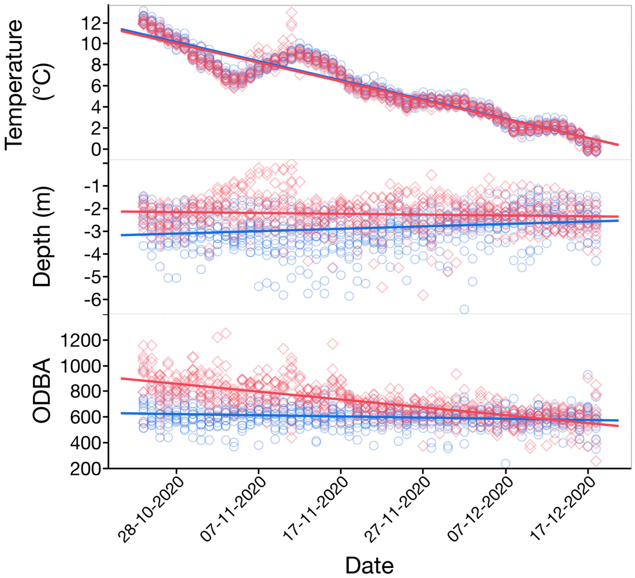

FIGURE 3 Relationships between the date and the biologging data for male (red diamonds; $n=11$) and female (blue circles; $n=12$) northern map turtles from Opinicon Lake, Ontario, Canada. For temperature and depth, each point represents the daily mean for a turtle. For the locomotor activity (ODBA), each point represents the daily sum for each turtle.

We further examined the patterns in depth and ODBA every minute between 0700h and 1700h for the period during which the burying behavior was observed (24–31 October) which also corresponds to the period during which the differences in mean daily depth and ODBA were most pronounced (Figure 4). Females generally remained at the bottom for most of the day and their activity appeared to be associated with rapid vertical migrations to reach the surface (Figure 4). Males, in contrast, showed higher levels of locomotor activity (ODBA) and greater fluctuations in depth, and their vertical movements were not clearly associated with surfacing (Figure 4). To assess the intra-individual variation in depth, we calculated the coefficient of variation for each turtle for the period 24–31 October using the depth averaged for each minute. The CV in depth ranged from 12% to 40% (mean = 21.5%) for the 12 females and from 34% to 59% (mean = 43.4%) for the 11 males. The mean CV in depth between the sexes differed significantly (t-test: $t_{(21)}=6.87$, $p<.001$) with females remaining at more consistent depths than males (Figure 5).

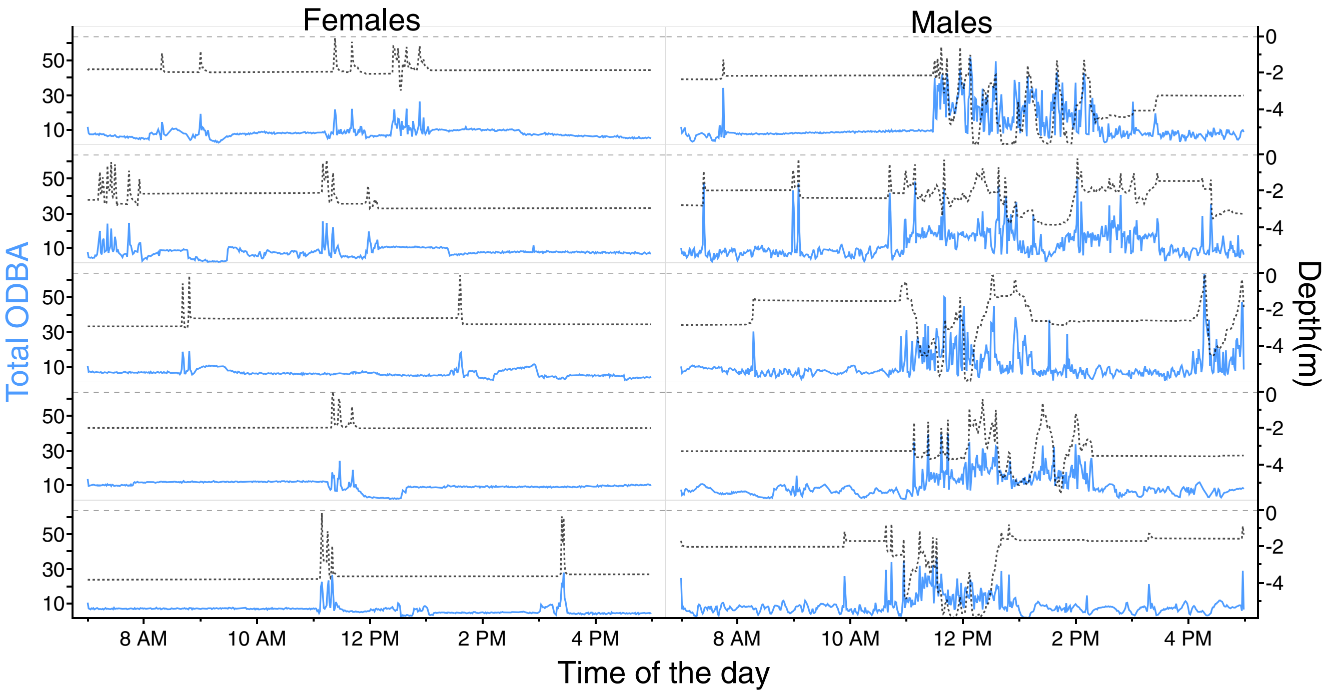

FIGURE 4 Locomotor activity (ODBA; solid blue line) and depth (dotted black line) patterns for five male and five female northern map turtles from Opinicon Lake, Ontario, Canada on 26 October 2020. This day was chosen because it corresponds to the period during which the female burying behavior was observed. Depth was measured every second and averaged for each minute. ODBA was measured every tenth of a second and averaged for each minute. The gray dashed line indicates the water surface on the depth axis.

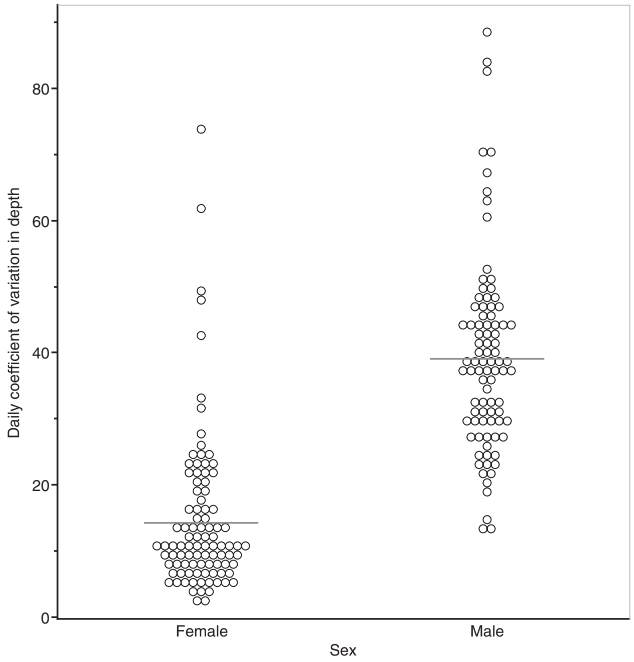

FIGURE 5 Daily coefficients of variation in depth for male ($n=11$) and female ($n=12$) northern map turtles from Opinicon Lake, Ontario, Canada between 24 and 31 October 2020. Depth was measured each second between 0700 and 1700 h. Each point represents the coefficient of variation for one turtle for one day. The gray lines show the mean coefficients of variation for each sex.

4 | DISCUSSION

Our video analyses revealed that female northern map turtles are heavily solicitated by males during the mating season with 56% of active females being pursued by at least one male. Male northern map turtles can be persistent suiters. For instance, in the experimental data we re-analyzed here, we recorded 17 mating attempts between a live male and a female decoy (Bulté et al., 2021). One male spent 126 min on the female decoy, 31 of which were spent trying to mate with it. This individual appeared to be an extreme case, but even with that male excluded, the mean time a live male spent mounted on a female decoy in a mating attempt was 9.6 min (range: 1–28 min). Considering that females are being pursued by males more than half of the time, and that males can spend several minutes attempting to mate, females appear to be heavily solicited by males while they are in the vicinity of their hibernacula. Moreover, male northern map turtles occasionally bite females as part of mating attempts, suggesting that some males punish unreceptive females (Bulté & Blouin-Demers, n.d.). Collectively, these observations indicate that exposed females experience harassment by males. The cost of resisting frequent and sometimes persistent or aggressive mating attempts may thus be high for females. Moreover, intense solicitation by males may increase the risk of predation for females as seen in other taxa (Kelly et al., 1999; Magnhagen, 1991; Rowe, 1994). Mass turtle predation by river otters (*Lontra canadensis*) was documented in winter at our study site (Bulté et al., 2023), but predation can also occur during the mating season. We observed a river otter attack one decoy during a mate choice experiment at the study site.

The biologging data were consistent with our hypothesis that burying serves as a male avoidance tactic for female northern map turtles. Locomotor activity in females was relatively constant during the sampling period, while the activity of males declined steadily. The strong effect of date on the locomotor activity of males was likely driven by the rapid cooling of the lake during the sampling period. Logger temperature and date were strongly correlated ($r=0.94$) during that period. The fact that females minimally reduced locomotor activity over the same period suggests that females, contrary to males, reduce their activity early on for reasons other than decreasing temperatures. The relatively high male locomotor activity at the beginning of the sampling period likely reflects mate searching and mating activity. Courtship and mating behaviors are regularly observed at the overwintering sites in the fall. Studies on other temperate turtles have also reported that males remain active for longer than females in the fall to increase mating opportunities (Moldowan et al., 2018; Morreale et al., 1984; Thomas et al., 1999).

It is unlikely that foraging contributed to the measured locomotor activity because turtles do not appear to forage regularly in late fall. In Opinicon Lake, turtles captured in late fall and early spring rarely defecate while being held in captivity (Bulté, personal observation). Turtles likely stop feeding in the fall to prevent undigested food from rotting in their digestive tract as the water rapidly cools. Indeed, freshwater turtles have a slow digestive turnover, especially at low temperatures (Parmenter, 1981). For instance, at 16°C, it can take more than 4 days for food to transit through the gut of painted turtles (Parmenter, 1981). If feeding is limited in the fall, buried females would not incur a cost in terms of lost foraging opportunities. Movements between locations is another potential source of locomotor activity, but no turtles equipped with radio-transmitters left the overwinter site before the spring. Leaving the overwintering site late in the fall would be risky as very few sites allowing turtles to meet their demand for oxygen and avoid winter predation are available (Bulté et al., 2023). The ecological and physiological requirements of map turtles in winter may thus constrain them to remain in areas where male solicitation is high.

Females may reduce activity in the fall to save energy for the nesting season the following summer. In temperate areas, female turtles typically start their follicular development in the fall (Congdon & Tinkle, 1982; Kuchling, 1999; McPherson & Marion, 1981). By remaining relatively inactive, females may be able to increase the amount of energy they allocate to follicular development. Energy saving does not explain the use of slightly deeper water by females, however, nor their burying behavior. The use of deeper water and burying could reduce energy expenditure if they translated into lower body temperatures, but there were no differences in temperatures between males and females. It may also be tempting to surmise that females reduce activity to save energy in preparation for several weeks of submergence without feeding, but energy availability does not appear to be a limiting factor in overwintering turtles as their energy expenditures in winter are minimal (Crawford, 1994; Jackson & Ultsch, 2010).

In our study population, 71% of clutches have multiple sires and the maximum number of sires per clutch is three (Banger et al., 2013). The number of sires per clutch is thus markedly lower than the potential mating rate of females as assessed by the intensity of male solicitation. The number of sires may be limited by sperm competition or by cryptic female choice rather than by mating rate. The discrepancy between the number of sires and the potential mating rate of females, however, could also indicate that female northern map turtles control mating rate to some extent. Burying could reduce visual detection by males and previous experiments using female decoys (Bulté et al., 2018, 2021) showed that visual cues are sufficient for males to locate exposed females and to elicit courtship and mating behaviors. It is unclear if other cues, such as pheromones or other chemicals, are also involved in mate searching, but burying could also mask such cues. Further work is needed to determine if and how sperm competition, cryptic female choice, and mate resistance/avoidance affect polyandry in this species.

We observed the burying behavior only during the fall mating season, but it may also occur in the spring. If burying is indeed a male avoidance tactic, we expect that it should be more prevalent in fall than in spring because female map turtles can avoid males through other means in the spring. At our study site, turtles resume basking as soon as the lake is ice-free and can spend several hours basking every day (Bulté & Blouin-Demers, 2010). As far as we know, courtship and mating only occur in water, so basking females should not be solicited by males. Moreover, adult females form large basking aggregations and few males bask with them, which may indicate a form of sexual segregation. Most turtles overwintering at the communal site disperse to summer home ranges in early spring (Carrière et al., 2009). Females may thus avoid male solicitation in spring by dispersing early from the overwintering site. Such a strategy is employed by female red-sided garter snakes (*Thamnophis sirtalis parietalis*) at communal hibernacula (Shine et al., 2005). Unfortunately, we do not have data to test formally for sexual differences in the timing of arrival to and dispersal from the communal overwintering site.

The reproductive ecology of northern map turtles is similar in many respects to that of other species in which male density is high and females are briefly aggregated around an essential resource such as an overwintering site or a breeding pond that cannot be defended or monopolized by males. Such mating systems include red-sided garter snakes at communal overwintering sites (Shine et al., 2000, 2005) and European common frogs (*Rana temporaria*) at breeding ponds (Dittrich & Rödel, 2023). In these mating systems, females experience high levels of male harassment and use tactics to avoid males. Here, we provided evidence strongly suggesting that female northern map turtles avoid intense solicitation and potential harassment by males by burying themselves in lake sediments. This behavior appears to be a low-cost solution for females to reduce the costs of resistance and mating while they are constrained to spend the winter at sites with high male densities.

AUTHOR CONTRIBUTIONS

Grégory Bulté: Conceptualization; Data curation; Formal analysis; Visualization; Writing – original draft; Methodology; Investigation; Project administration; Writing – review & editing; Funding acquisition; Resources. **Jessica A. Robichaud:** Data curation; Formal analysis; Methodology; Writing – review & editing; Investigation. **Steven J. Cooke:** Supervision; Project administration; Writing – review & editing; Resources; Funding acquisition; Methodology. **Heath A. MacMillan:** Resources; Funding acquisition; Writing – review & editing; Supervision; Project administration; Methodology. **Gabriel Blouin-Demers:** Conceptualization; Writing – original draft; Writing – review & editing; Resources; Formal analysis; Funding acquisition.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in DRYAD at https://datadryad.org/stash/share/w0VG1TAODCoUvAw3HYpQykeEK6UnyAxgclX_W7tsPTA

ORCID

Grégory Bulté https://orcid.org/0000-0002-7066-3526

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