RESEARCH ARTICLE



Free-ranging male northern map turtles use public information when interacting with potential mates

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Abstract

Sperm competition is prevalent in animals, and many adaptations have evolved to reduce its risk. Males can reduce the risk of sperm competition by using public information when interacting with potential mates. Specifically, males can reduce sperm competition by avoiding females already affiliated with rival males. We tested this hypothesis in a population of wild northern map turtles (Graptemys geographica), a gregarious species with seemingly prevalent sperm competition. We used 3D-printed decoys and underwater videography to record the response of free-ranging males to female decoys affiliated or not with rivals. More visits were made by males to female decoys when rivals were present, suggesting a form of eavesdropping during mate selection. Males were more likely to interact with the female decoy, however, when rivals were absent, suggesting that they behave to reduce sperm competition. Moreover, the types of interactions differed between the accompanied and the unaccompanied female decoys, indicating an audience effect during male-female interactions. Finally, males interacted more with the male decoys than with the female decoys in the treatment with rivals, indicating a yet unclear form of male-male interaction. Collectively, our results suggest that free-ranging male northern map turtles use public information for mate selection and to reduce sperm competition.

KEYWORDS

audience effect, eavesdropping, non-independent mate choice, Sperm competition

| INTRODUCTION 1

Competition for mates has many evolutionary consequences. For instance, competition for mates has led to the evolution of extravagant ornaments and of elaborate courtship behaviors (Andersson, 1994). In addition, competition for mates has favored the formation of new species through the reinforcement of reproductive barriers (Coyne & Orr, 2004).

Competition for mates can take many forms. Males can compete for access to mates through displays, scrambles, and combats. Competition can also continue after mating has occurred in the form of sperm competition (Andersson, 1994; Parker, 1970). Sperm competition is widespread in animals (Birkhead, 1998) and numerous

adaptations have evolved in response. Examples of such adaptations include enlarged testes to produce voluminous ejaculates (Lüpold et al., 2020), copulatory plugs (Schneider et al., 2016), mate guarding to prevent subsequent mating (Burdfield-Steel & Shuker, 2014; Chaudhary et al., 2017; Willis & Dill, 2007), and even specialized structures and behaviors to remove the sperm of rivals from the reproductive tract of females (Davies, 1983; Galeotti et al., 2008; Waage, 1979).

Males can reduce sperm competition by exploiting information inadvertently generated by interactions among conspecifics. Such public information (Danchin et al., 2004) influences mate choice decisions in a range of animals leading to non-independent mate choice (NIMC; Davies et al., 2020; Jones & DuVal, 2019; Vakirtzis, 2011). For instance, the presence of sexual rivals near a prospective mate is a

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form of public information that males can use when selecting mates. In fact, in some species, males decrease their preference for previously preferred females when rivals are present (Dubois & Belzile, 2012; Plath et al., 2008, 2009; Wong & McCarthy, 2009; Ziege et al., 2009). This reduced preference for females accompanied by rival males presumably reduces the risk of sperm competition.

Sperm competition appears to be common in reptiles as suggested by the high prevalence of multiple paternity in this group (Blouin-Demers et al., 2005; Friesen et al., 2020; Uller & Olsson, 2008). Moreover, mating in some species of reptiles occurs while individuals are aggregated at rookeries (e.g., Lee et al., 2018 or communal hibernacula (e.g., Shine et al., 2001). These often-dense aggregations create both opportunities for polygyny, and thus sperm competition, as well as for public information to be generated and used by males competing over mates. In such settings, NIMC may be used by males to reduce sperm competition. Yet, we are unaware of any studies on NIMC in reptiles and two recent meta-analyses on this topic did not report any studies on reptiles (Davies et al., 2020; Jones & DuVal, 2019).

Most studies of NIMC have been conducted in captivity and mainly on fish (Davies et al., 2020; Jones & DuVal, 2019). Laboratory studies permit a tight control over confounding variables potentially affecting mate choice (e.g., age, size, health status, mating history, personality, etc.), but they may not always emulate all the factors influencing mate choice in the wild such as habitat structure or natural population density (Scauzillo & Ferkin, 2019). Moreover, the handful of model species from which our understanding of NIMC is derived may not represent the diversity of mating systems and environments that could influence the evolution and maintenance of NIMC in nature. Field studies of NIMC with non-model species can thus offer new insights into the evolutionary ecology of NIMC (Sapage et al., 2020).

The northern map turtle (Graptemys geographica) is a widespread species of freshwater turtle in eastern North America (Ernst & Lovich, 2009). Conditions for both intense sperm competition and NIMC are present in this species. Northern map turtles form dense overwintering aggregations (Ultsch et al., 2000), and mating takes place in late fall and early spring while turtles are aggregated (Bulté et al., 2018). In temperate areas, it is common for freshwater turtles to mate both in the fall and in the spring and females can store sperm for weeks until fertilization (Kuchling, 1999). Sperm storage by females may promote sperm competition and cryptic female choice. During the mating season, females are commonly observed surrounded by two or three males simultaneously (Figure 1) and females mate with multiple males. Indeed, Banger et al. (2013) reported that at least 71% of clutches in northern map turtles are sired by two or three males, indicating that sperm competition is common in this species. Based on this information, we expected male map turtles to use public information to minimize sperm competition.

Studying the reproductive behavior of freshwater turtles is challenging because courtship and mating occur underwater and wild turtles are skittish. Consequently, we know relatively little about these important behaviors (Liu et al., 2013). We recently successfully



FIGURE 1 Two male northern map turtles (*Graptemys* geographica) simultaneously interacting with a female. Such mating aggregations are common in spring and fall at communal hibernation sites in Lake Opinicon, Ontario, Canada

used 3D-printed decoys and underwater videography to show experimentally that free-ranging male northern map turtles prefer larger females (Bulté et al., 2018). Here, we used a similar approach to test the hypothesis that the presence of rivals influences mate choice in male northern map turtles in the wild. If males use public information to reduce sperm competition, we predicted that female decoys affiliated with rivals (male decoys) should be visited less by males. We also predicted that males should interact less with female decoys affiliated with rivals.

2 | MATERIALS AND METHODS

We conducted this experiment in spring 2017 at two communal hibernation sites used by northern map turtles in Lake Opinicon 130 km south of Ottawa, Ontario, Canada.

Our previous radio-telemetry work indicated that the two hibernation sites we studied here are the main hibernation sites in Lake Opinicon (Carrière et al., 2009). These two hibernation sites are also the focal capture sites for our long-term demography study initiated in 2003 (Bulté & Blouin-Demers, 2009) To date, we have captured and marked 649 males in Lake Opinicon, of which 485 (75%) were captured at least once in the vicinity of one of these two hibernation sites. The most males captured in a single year in the vicinity of these two hibernation sites were 127 in 2019 (Bulté, unpublished data). The two experimental sites thus contain a large sample of males that can safely be assumed to be representative of the whole male population in Lake Opinicon. Since 2003, we have captured and marked 966 females in Lake Opinicon. Of these, 621 (64%) have been captured at least once in the vicinity of one the hibernation sites and 28% of these captures were sexually mature individuals.

We used underwater action cameras to record the response or free-ranging male map turtles to female decoys (Bulté et al., 2018) under two treatments: not affiliated with rival males, and affiliated with three rival male decoys. In the latter treatment, the three male

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decoys were positioned 20 cm from the female decoy on either side and in front of it (Figure 2a). All decoys were created from preserved specimens using a 3D scanner and printer and painted by a wildlife artist as described by Bulté et al. (2018). The decoys were the size of mature individuals: the female decoys were 290 mm in maximum straight-line carapace length (method A in Iverson & Lewis, 2018) and the male decoys were 115 mm in maximum straight-line carapace length (Bulté et al., 2018).

We attached the decoys on custom built frames made of 3.81 cm diameter ABS pipe and mounted an action camera (GoPro Hero 3 equipped with a Wasabi battery) on a vertical member positioned above the decoys (Figure 2). We weighted the frames with four 1.3 kg diving weights. We positioned the female decoy near the center of the camera field of view (ca. 80 cm x 135 cm, see Video S1). We deployed both treatments simultaneously at the same hibernation site on 10 days between 14 April and 28 April 2017. The two treatments were haphazardly dropped to the bottom of the lake (ca. 2-4 m depth) and positioned 10 to 20 m from each other. We deployed the decoys daily between 7:00-8:00 and retrieved them between 18:00 and 19:00. The cameras recorded at a resolution of 720 x 1280 pixels for an average of 9 h (range 6-10 h) per deployment.

One of the authors (BH) examined the footage in Windows MediaPlayer and extracted several behavioral variables. To assess the general attractiveness of females affiliated or not with rivals, we recorded the total number of male visits as well as the duration of each visit. A visit was defined as a male entering and leaving the field of view. We used the number of visits and not the number of males because we cannot exclude the possibility that a male entered the field of view more than once because the video resolution was insufficient to identify males individually. There were some instances, however, in which the same male clearly left and re-entered the field of view within seconds. In such instances, a single visit was recorded. We assumed that repeated visits by the same individual were relatively rare given the high density of males at our sites, but we could not verify this assumption. We also recorded the duration of each visit in seconds. A visit began when a male was entirely within the field of view and ended when it had entirely left it. We predicted that female decoys affiliated with rivals should receive fewer and shorter visits by males.

We also recorded three types of interactions by males with the decoys (Figure 2 and Video S1). Males were often observed extending their necks toward the decoys (male and female) often moving toward the decoys at the same time. We coined these interactions Close Range Investigations (CRI) and recorded the number of such interactions in each treatment. To be recorded as a CRI, the focal male had to be one body length or less (Figure 2b) from a decoy while performing the behavior. We predicted that females affiliated with rivals should receive fewer CRI than females on their own. We also recorded the area of the decoy the focal male was extending its neck toward as lateral (between the front and hind legs), anterior (between the front legs), or posterior (between the hind legs). The courtship and mating behaviors of northern map turtles are poorly documented, but males have been reported to face and touch the female head and cloaca as part of their courtship (Ernst & Lovich. 2009). We thus predicted that CRI should be more frequently directed at the head (anterior) and at the cloaca (posterior) than at the sides (lateral) of female decoys. If a focal male performed more than one CRI of the same decoy, we counted them as one CRI for that focal male. Finally, we recorded the number of instances a focal male mounted or attempted to mate with the female decoy. A focal male was recorded as mounting the decoy if at least two legs were placed anywhere on the decoy (Figure 2c). If a focal male mounted the decoy more than once, we counted only one mounting event for that focal male. A mating attempt was recorded when a male assumed a mating position on the model as shown in Figure 2b. We predicted that female decovs affiliated with rivals should be mounted less often and receive fewer mating attempts than females not affiliated with decoys.

We tested for a difference in visit duration between the two treatments with a Wilcoxon-Mann-Whitney test because the assumptions of normality and homoscedasticity were violated. We tested whether each behavior (visits, CRI, mountings, and mating

FIGURE 2 (a) Diagram of the set-up used in the experiment to investigate mate selection in northern map turtles (*Graptemys geographica*) in Lake Opinicon, Ontario, Canada. The female decoy is depicted in dark gray and the male decoys in pale gray. (b) Examples of a male attempting to mate with a female decoy and of a male performing a closerange investigation of the female decoy. (c) Example of a male mounting (but not mating with) the female decoy





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attempts) were evenly distributed between the two treatments with Pearson's Chi-Square Tests. If the presence of rivals did not affect the behavior of males, we expected the number of observations to be evenly distributed between the two treatments. We also compared the frequency of the area of the decoy investigated between the two treatments with a Pearson's Chi-Square Test. All statistical analyses were performed in JMP version 16 (SAS Institute Inc., Cary, NC, 1989–2021).

This research was approved by the Carleton University Animal Care Committee (protocol no 10267) and conducted with a permit from the Ontario Ministry of Natural Resources and Forestry (permit no 1085909).

3 | RESULTS

Over the 10 days during which we deployed decoys, we recorded 181.5 h of footage in which we observed 775 visits of the field of view by free-ranging male map turtles. Males visited the treatment without rivals (n = 307; 39.6% of observations) significantly less ($\chi^2_{,1}$ = 33.44; *p* < 0.001) than the treatment with rivals (n = 468; 60.4% of observations).

The mean duration of a visit ranged from one second to nearly two and a half h. The latter was a clear outlier as the male remained immobile for most of the time in the field of view. This observation was thus excluded from the analysis. Excluding this outlier, the maximum time in the field of view was 31 min. The ranked distributions of the duration of a visit did not differ between the two treatments (Wilcoxon–Mann–Whitney test: z = 0.683; p = 0.495).

We recorded 228 CRI of a female decoy by a male. Males performed CRI in the treatment without rivals (n = 132; 57.8% of observations) significantly more ($\chi^2_{,1}$ = 5.68; *p* = 0.0171) than in the treatment with rivals (n = 96; 41.9% of observations).

In the treatment with rivals, 189 of the visits resulted in at least one CRI by the focal male. In 62 (32.8%) of the cases, the focal male investigated the female decoy. In 93 (49.2%) of the cases, the focal male investigated at least one of the male decoys. Finally, in 34 (18.0%) of the cases, the focal male investigated at least one male decoy as well as the female decoy.

In cases in which the male investigated a female decoy, the frequency of the area of the decoy investigated differed between the two treatments ($\chi^2_{,2} = 11.89$; p = 0.0026). In the treatment without rivals, we recorded 38 (30.6%), 45 (36.3%), and 41 (33.1%) investigations of the anterior, lateral, and posterior areas, respectively (Figure 3). These frequencies did not differ significantly from one another ($\chi^2_{,2} = 0.597$; p = 0.742). In the treatment with rivals, we recorded 31 (34.1%), 48 (52.7%), and 12 (13.2%) investigations of the anterior, lateral, and posterior area, respectively (Figure 3). These frequencies differed significantly from one another ($\chi^2_{,2} = 21.38$; p < 0.001). Overall, focal males investigated the posterior area of the female decoy more frequently in the treatment without rivals than in the treatment with rivals, but investigated the lateral area less frequently (Figure 3).

We observed 55 instances in which the focal male mounted the female decoy. Males mounted the female decoy in the treatment without rivals (n = 30; 54.5% of observations) at the same frequency ($\chi^2_{,1} = 0.454$; p = 0.500) as in the treatment with rivals (n = 25; 45.4% of observations; Figure 4).

We observed 17 mating attempts by a focal male. Males attempted to mate with the female decoy in the treatment without rivals (n = 11; 64.7% of observations) at the same frequency ($\chi^2_{,1} = 1.47$; p = 0.225) as in the treatment with rivals (n = 6; 35.4% of observations; Figure 4).

4 | DISCUSSION

Our goal was to test whether the presence of rivals affects the decision of free-ranging male northern map turtles to interact with prospective mates in the wild. We predicted that males should interact less with females affiliated with rivals given that sperm competition appears to be strong in this species (Banger et al., 2013). Our results partially support this prediction but revealed that male map turtles also use public information for reasons other than to limit sperm competition.

The treatment with rivals attracted 20% more visits by males than the treatment without rivals which is, at first glance, contrary to our prediction. When only examining the data from the treatment with rivals, however, it became apparent that many visiting males were in fact attracted by the male decoys rather than the female decoy. Indeed, only 33% of the close-range investigations in the treatment with rivals were directed toward the female decoy, but nearly half of these investigations were directed toward the male decoys.

Male map turtles may cue on rivals to locate receptive females as is the case in other animals (Clark et al., 2012; Milner et al., 2010; Webster & Laland, 2013). Such eavesdropping behavior may be useful for male map turtles because females are much larger than males and can outswim them (Pluto & Bellis, 1986). A female affiliated with males may thus be a reliable indicator of receptivity. This strategy could explain why the total number of visits is higher in the treatment with rivals, but it cannot explain why most CRIs were directed toward the male decoys rather than the female decoy.

Males may have interacted with decoys of rivals for sexual or social reasons. The male-male interactions may be part of a rival assessment behavior (e.g., Yorzinski et al., 2017). If males are indeed adopting behaviors to limit sperm competition, assessing rivals before investing in courtship and mating should be advantageous. Males may also attempt to interfere with the courtship of their rivals. Such behavior occurs in birds where eavesdropping males interfere with the courtship of rivals, presumably to reduce competition (Balsby & Dabelsteen, 2005; Searcy & Nowicki, 2006). This form of interference possibly occurs in male northern map turtles. We did not observe aggressive behaviors between the focal males and the male decoys, however, nor between males when more than one male was interacting with the female decoys. Moreover, the focal males



FIGURE 3 Number of close-range investigations (CRI) of a northern map turtle (*Graptemys geographica*) female decoy by free-ranging males without and with three rival male decoys in an experiment conducted in Lake Opinicon, Ontario, Canada. The CRI are split by the area of the body of the female decoy investigated: anterior in white, lateral in pale gray, posterior in dark gray. The female decoys are depicted in black and the focal males in gray. The frequency of the area of the decoy investigated differed between treatments ($\chi^2_{,2} = 11.89$; p = 0.0026)



FIGURE 4 Number of mountings (white) and mating attempts (gray) of a northern map turtle (*Graptemys geographica*) female decoy by free-ranging males without and with three rival male decoys in an experiment conducted in Lake Opinicon, Ontario, Canada. The female decoys are depicted in black and the focal males in gray. The frequencies of mountings and mating attempts did not differ significantly between treatments (mountings: $\chi^2_{,1}$ = 0.454; p = 0.500; mating attempts: $\chi^2_{,1}$ = 1.47; p = 0.225)

physically interacted with the male decoys in only 9.2% of the CRI (13/140). If males do indeed try to interfere with their rivals, it appears to be rare.

Males may have been attracted to male decoys for social, rather than sexual, reasons. The social behaviors of reptiles are poorly studied, but these animals are arguably more social than previously recognized (Doody et al., 2013). A similar experiment to ours, in which wild turtles would be presented with groups of males with and without a female, would allow to distinguish whether males are attracted to one another for social or sexual (i.e., assessment or interference) reasons.

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Although we recorded more visits by males in the treatment with rivals, males were 16% more likely to investigate the female decoy in the treatment without rivals than the female decoy affiliated with three rivals. These results indicate that males are less interested in females affiliated with rivals, as we predicted based on the high potential for sperm competition in map turtles. The trends in the numbers of mountings and of mating attempts are also consistent with this interpretation, but the differences between treatments were not significant. In the case of the number of mating attempts, the effect size was large (i.e., 65% of observations in the treatment without rivals), but our statistical power was low due to our small number of observations (n = 17). Overall, our results are consistent with several studies of male mate choice in which males avoided females affiliated with rivals (Dubois & Belzile, 2012; Plath et al., 2008, 2009; Wong & McCarthy, 2009; Ziege et al., 2009), but it is to the best of our knowledge the first time this is demonstrated in a reptile.

We also found that wild males interacted differently with the decoys when rivals were present. Most notably, males were 20% less likely to investigate the posterior area of the female decoy when rivals were present, and 17% more likely to investigate its lateral area. In many freshwater turtles, courtship begins with the male nosing or touching the female's cloacal area with its snout (Liu et al., 2013). This behavior could be involved in mate recognition and in the assessment of female receptivity (Kuchling, 1999). The difference in male behavior between treatments clearly indicates that males are aware of the presence of conspecifics when interacting with a female. Such audience effects have been reported in a range of animals (Auld & Godin, 2015; Dubois & Belzile, 2012; dos Santos et al., 2017). In laboratory studies, males can reverse their original preference for females in the presence of an audience of rivals (Auld & Godin, 2015; Dubois & Belzile, 2012; Plath & Schlupp, 2008). This response to an audience is interpreted as a form of deception to lead rivals away from a preferred mate. Unfortunately, we currently know too little about the courtship behavior of map turtles to speculate on the potential adaptative significance of the audience effect we observed in our study.

Underwater videography and 3D-printed decoys have become common tools to study animal behavior in the wild (Walker & Humphries, 2019; Struthers et al., 2015). Our study highlights the fruitfulness of combining these tools to study the behavior of otherwise difficult to observe species. Moreover, this approach can alleviate some of the biases inherent to many studies with captive animals, such as rearing history and acclimation (Webster & Rutz, 2020). This approach, however, has some limitations and potential biases. One inherent limitation is the inability to identify the individuals interacting with the decoys. While identification may be achieved with higher video resolution, finer details in underwater videography are often lost because of low light levels. A promising avenue to identify individuals is to combine our approach with Passive Integrated Transponders (PIT). If enough individuals are marked with PIT tags,

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it would be possible to record the number of individuals visiting a decoy and the number of visits per individual by integrating PIT recorders in the decoys.

Exposing free-ranging animals to decoys also potentially induces biases. In the present case, self-selection and genetic background are potential sources of bias. Our data and conclusions are derived only from individuals that "chose" to interact with the decoys. Although our decoys were clearly perceived as conspecifics by males, we cannot exclude the possibility that individuals with less exploratory or more neophobic personalities were more reluctant to interact with them. Unfortunately, we do not know how much personality varies among individuals in map turtles, nor if that variation affected our results. We did observe a high number of interactions, however, and thus feel confident that our results did capture a biologically meaningful subset of the personalities present in the population. It should also be noted that our conclusions are derived from a single, albeit large, population. There is nothing to suggest that our study population is atypical, but the northern map turtle has an extensive range (Ersnt & Lovich 2009) and spatial variation in the ecology and demography of the species is expected. Such variation may have led to different reproductive strategies. Nonetheless, our predictions were based on documented aggregation and multiple paternity. Both phenomena appear to be characteristic of the species and of many species of freshwater turtles. For instance, multiple paternity is ubiquitous in turtles indicating that sperm competition must be too (Olsson et al. 2008). Moreover, aggregation for hibernation appears to be typical in northern map turtles. Indeed, this species hibernates communally in Wisconsin (Vogt, 1980), Vermont (Ultsch et al., 2000). Pennsylvania (Pluto & Bellis, 1988). Maryland (Richards-Dimitrie, 2011), and Ontario (Carrière et al. 2009).

In conclusion, we showed that male northern map turtles are influenced by public information when choosing mates and adjust their behaviors in ways that are consistent with attempts to reduce sperm competition. Our results also suggest that males use eavesdropping to locate receptive females and are influenced by an audience when interacting with prospective mates. Our study is, to the best of our knowledge, the first demonstration of non-independent mate choice in a reptile and one of very few to document this phenomenon in the wild.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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