



Sex, shells, and weaponry: coercive reproductive tactics in the painted turtle, *Chrysemys picta*

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Abstract

Males and females have divergent reproductive interests arising from their unequal investments in offspring. This sexual conflict drives an antagonistic arms race that influences sex-specific reproductive success. Alternative reproductive tactics are expected in long-lived species for which the reproductive strategy that maximizes mating success could differ across body sizes. The mating strategy of the painted turtle (*Chrysemys picta*) has been characterized as an elaborate and amiable male courtship display during which males use their elongate foreclaws to stroke females, coupled with female mate choice. Contrary to this long-held understanding, in situ field observations and experimental trials from our long-term study in Algonquin Provincial Park, Canada, demonstrate that males also exhibit an alternative, coercive mating strategy. Males are equipped with sexually size dimorphic tomiodonts, tooth-like cusps of the beak, as well as a weaponized anterior shell, with which they wound the head and neck of females. Behavioral trials during the breeding periods showed that male reproductive tactics shift from courtship (foreclaw display) to coercion (striking, biting, and forced submergence) across ontogeny, and male size predicts the occurrence and frequency of coercive behavior. We found phenotype-behavior matching whereby small males invest in putatively ornamental foreclaws used for courtship and large males invest in weaponry for coercion, challenging existing knowledge of this well-studied species. As a group with a long evolutionary history and varied mating systems, Testudines are a particularly interesting taxon in which to ask questions about mating system evolution.

Significance statement

Alternative reproductive tactics are hypothesized for long-lived species. We quantified a shift from apparent courtship to coercive tactics during the reproductive lifespan of a well-studied freshwater turtle. Male painted turtles (*Chrysemys picta*) have sexual weapons that are used to promote female acquiescence. Using behavioral trials with turtles from a long-term study population, we demonstrate that males match their morphology (ornament/weapons) to reproductive behavior (courtship/coercion) as their reproductive tactics shift. Our findings hint at the behavioral complexity of aquatic turtles, a challenging and often-overlooked group in behavioral studies.

Keywords Alternative reproductive tactics · Mating strategy · Sexual conflict · Sexual dimorphism · Sexual weapon · Titillation

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Introduction

Sexual conflict and male-female antagonism Males and females have divergent reproductive interests arising from the unequal, often female-biased, investment in offspring (Trivers 1972; Andersson 1994). The reproductive potential of a female is limited by her ability to reduce costs associated with mating and to invest energy and time into offspring (Bateman 1948; Andersson 1994; Rowe 1994; Rowe et al. 1994; Andersson and Iwasa 1996). In contrast, males may invest relatively little into reproduction and incur relatively low mating costs compared to females, yet males can achieve high reproductive success by mating with multiple females (Gavrilets et al. 2001; Chapman et al. 2003). This sexual

conflict can result in an antagonistic coevolutionary arms race through sexual selection (Dawkins and Krebs 1979; Parker 1979; Clutton-Brock and Parker 1995; Arnqvist and Rowe 2002) whereby each sex strives to maximize its reproductive potential while attempting to minimize the reproductive costs associated with mating, parental investment, and offspring care. As a result of competing interests, both sexes are expected to evolve adaptations that influence reproductive outcomes in their favor (Rice 1998; Chapman et al. 2003). Females' selection of and resistance to mates are expected to promote male behavioral and/or morphological traits that exploit or overcome female preferences. In a sexually antagonistic arms race, males are expected to resist female attempts at reproductive cost-sharing, and may do so by adopting alternative (coercive) reproductive tactics and/or sexual weaponry.

Sexual selection and coercion Research on sexual selection has largely focused on mate choice, male-male contests, and sperm competition, although many alternative and non-mutually exclusive mechanisms exist, such as scramble competition, and notably, sexual coercion (Andersson 1994; Andersson and Iwasa 1996). Sexual coercion is the use of force, or threat of force, by a male to increase chances that a female will mate during her fertile period and decrease chances that she will mate with other males (Smuts and Smuts 1993; Andersson and Iwasa 1996). Females incur a cost from the sexually coercive behavior of males (Smuts and Smuts 1993), which can take several forms: forced copulation, during which a male physically restrains a female while achieving forceful copulation; harassment, when males make repeated attempts to copulate with females who are coaxed into mating due to costs created by harassment; and intimidation, when males punish females that resist copulation, in turn increasing the chances that a female will be accepting of future mating attempts (Clutton-Brock and Parker 1995; Andersson and Iwasa 1996).

Reproductive tactics can be highly dynamic, condition- and context-dependent. For instance, male guppies (*Poecilia reticulata*) shift mating tactics from courtship to coercion in response to female behavior and predation risk (Magurran and Nowak 1991). Despite sexual coercion being the dominant mating tactic of male mosquitofish (*Gambusia holbrooki*), females are still capable of some mate choice, demonstrating that these two tactics can co-exist (Bisazza et al. 2001). Female gartersnakes (*Thamnophis sirtalis*) experience cryptic coercion whereby males exploit features of female respiratory anatomy, physiology, and antipredator behavior to accomplish forced insemination (Shine et al. 2003). A growing number of examples of sexually coercive mating systems suggest that coercion is an important male reproductive tactic and mechanism of sexual selection.

Alternative and coercive reproductive tactics Alternative reproductive tactics refer to multiple ways to obtain fertilizations by males and females (Gross 1996; Taborsky et al. 2008). The traits that form the basis of alternative reproductive tactics, whether morphological (e.g., body size, weapons) or behavioral (e.g., courting versus sneaking males), often have dichotomous distributions, and individuals typically allocate resources to one or the other at a given time to maximize potential reproductive success (Brockmann 2001; Taborsky et al. 2008). Competing reproductive tactics are expected to result in exaggeration of sexually selected characters (e.g., sexual dimorphism in body size), and development of weapons, and/or costly ornaments (Neff 2001). Phenotype-behavior matching promotes complementarity of traits and mating tactics. For example, male body size and the presence of horns in the dung beetle (*Onthophagus* spp.) are related to fighting vs. non-fighting tactics during mating (Kotiaho and Tomkins 2001). Alternative reproductive tactics within an individual or population shift in response to fitness optima, varying with ontogeny, social ranking (e.g., dominant versus subordinate), physical condition, and local environmental conditions (e.g., competitors, density, sex ratio, resource availability; Rowe et al. 1994; Halliday and Tejedo 1995; Gross 1996; Alonzo et al. 2000; West-Eberhard 2003; Westneat and Stewart 2003; Taborsky et al. 2008). In particular, long-lived species that demonstrate indeterminate growth, such as Testudines (Congdon et al. 2003; Armstrong et al. 2018; but see Congdon et al. 2013), are expected to shift reproductive tactics across their lifetime as tactics that maximize mating success may differ across body sizes (Olsson and Shine 1996; Koga and Murai 1997; Angeloni and Bradbury 1999; Thomas 2002; Leary et al. 2005). In this paper, the distinction between reproductive tactic and strategy (Dominey 1984; Gross 1996) is not made and the two terms are treated synonymously (see discussion by Taborsky et al. 2008).

Reproductive behavior of Testudines and the painted turtle as a case study As a group with a rich evolutionary history and varied mating systems, Testudines are an interesting taxon in which to ask questions about mating system evolution. Available literature hints that the behavior and social systems of Testudines are complex (e.g., Kramer 1989; Pearse and Avise 2001; Davis and Burghardt 2007, 2011, 2012; Burghardt 2013; Hites et al. 2013; Brejcha and Kleisner 2016); however, preconceived, albeit unfounded, notions of behavioral simplicity in this taxon and difficulties associated with studying the cryptic habits of aquatic species have hampered detailed behavioral investigations of wild Testudines. There have been longstanding appeals for published studies of testudine reproductive biology and behavior (Carpenter and Ferguson 1977; Harless 1979; Berry and Shine 1980; Liu et al. 2013), but most reports are anecdotal and lack the replication necessary for rigorous hypothesis testing.

Widespread polygyny, intensive energetic reproductive investment, and the absence of parental care by female Testudines establish clear grounds for sexual conflict. In general, female turtles likely invest more into reproduction than males. In painted turtles (*Chrysemys picta*), for example, female reproductive effort—including courtship, mating, egg production, and nesting—has been estimated to require 48% of the annual energy budget, with egg production alone accounting for 14% of the total (Congdon et al. 1982). Although mate searching and courtship are purported to be energetically expensive for males (Jackson and Davis 1972; Kramer 1989; Kramer and Burghardt 1998; Pearse et al. 2002), this claim remains to be quantified. Testudines regularly demonstrate multiple paternity (Pearse and Avise 2001; Uller and Olsson 2008; Lee et al. 2018) and male painted turtles have higher reproductive variation than females by siring offspring from multiple clutches with multiple females within and across years (Pearse and Avise 2001; Pearse et al. 2002; McGuire et al. 2014). Reproductive investment by male painted turtles is limited to mate searching, pre-copulatory courtship display, and sperm production (Taylor 1933; Gibbons 1968; Ernst 1971; Ernst and Lovich 2009).

The mating tactics of Testudines are highly variable, spanning a spectrum from apparently amiable courtship to coercion (Berry and Shine 1980; Liu et al. 2013). Male aggression may be an effective mating tactic if coercive behaviors (e.g., chasing, biting, forced submergence) facilitate female receptivity or acquiescence through demonstration of male dominance or strength (Gibbons and Lovich 1990; Liu et al. 2013). Tortoises (Testudines: Testudinidae) are reputed for their coercive tactics (Hailey 1990; Sacchi et al. 2003; Golubović et al. 2018) and use of sexual weaponry (Auffenberg 1977; Tuma 2016). Among freshwater turtles, coercive mating tactics are often observed in species with a larger male body size, limited mobility, and an inability of non-receptive females to escape a suitor male (Berry and Shine 1980; Keevil et al. 2017). Conversely, aquatic and free-swimming species—notably members of the ecologically and taxonomically diverse Emydidae (Stephens and Wiens 2003)—typically demonstrate a larger female body size, male nuptial structures with associated courtship behavior, and high mobility (Berry and Shine 1980; Gibbons and Lovich 1990; Liu et al. 2013). Male pre-coital courtship behavior and/or display of nuptial structures (e.g., elongate foreclaws) are recognized as the principal mating strategy, along with female mate choice, for the Emydidae (Berry and Shine 1980; but see discussion by Gibbons and Lovich 1990; Bels and Crama 1994).

Painted turtles (Testudines: Emydidae: *Chrysemys* spp.) are one of the most well-studied freshwater turtles in North America and the world (Ernst and Lovich 2009; Valenzuela 2009; Lovich and Ennen 2013). The reproductive system of the painted turtle has been widely accepted as male courtship with female mate choice (Ernst 1971; Berry and Shine 1980;

Ernst and Lovich 2009). During aquatic breeding, males initiate a foreclaw display known as titillation, involving stroking the female with the sexually dimorphic claws of the forefeet (Taylor 1933; Cagle 1954; Ernst 1971; Ernst and Lovich 2009). Even Darwin (1871, citing Maynard 1869) remarked, “male of the mud-turtle of the United States (*Chrysemys picta*) has claws on his front feet twice as long as those of the female; and these are used when the sexes unite”. Receptive females may return display behaviors or sink to the substrate, which is followed by male mounting and copulation (Taylor 1933; Ernst 1971; Ernst and Lovich 2009). Painted turtles demonstrate a larger female body size, high mobility, and a free-swimming open water lifestyle. Thus, it has been suggested that coercive mating tactics would be improbable and unsuccessful (Berry and Shine 1980). However, some studies have provided evidence to the contrary (Thomas 2002; Liu et al. 2013), calling for an investigation into the apparently competing reproductive strategies of courtship and coercion in the painted turtle. We have identified strongly female-biased wounding patterns in our focal population (Moldowan et al. 2020) and multiple sexually dimorphic weapons, including tomiodonts (tooth-like cusps of the beak; Moldowan et al. 2016a, b, 2017) and carapace projections (Hawkshaw et al. 2019), of males (Fig. 1). Through these multiple lines of evidence, we hypothesized that coercive mating tactics are employed by male painted turtles.

Using behavioral trials during the breeding seasons, as well as morphological and ontogenetic data, we investigated whether male painted turtles demonstrate coercive tactics and, if so, under what circumstances. Based on our indirect evidence (Moldowan et al. 2016a, b, 2017, 2020; Hawkshaw et al. 2019), we hypothesized that the tomiodonts and anterior shell of male painted turtles are used as sexual weapons in female coercion. In addition, knowing that males develop weaponry across ontogeny (Moldowan et al. 2016b; Hawkshaw et al. 2019) and are long-lived, we hypothesized that males match their phenotype with reproductive behavior such that coercive behaviors occur at larger male body sizes, coincident with weapon development.

Methods

Study population and site Our study population of painted turtle occurs in two adjacent wetlands, Wolf Howl Pond and Wolf Howl Pond East (45° 34' N, 78° 41' W) in Algonquin Provincial Park, Ontario, Canada, where demographic and reproductive monitoring has taken place annually since 1978. Population size is approximately 260 adults total in these subpopulations (Samson 2003), each with a different population density: Wolf Howl Pond 96.8 turtles/ha and Wolf Howl Pond East 15.7 turtles/ha (MG Keevil, unpublished data; COSEWIC 2018). Individuals regularly

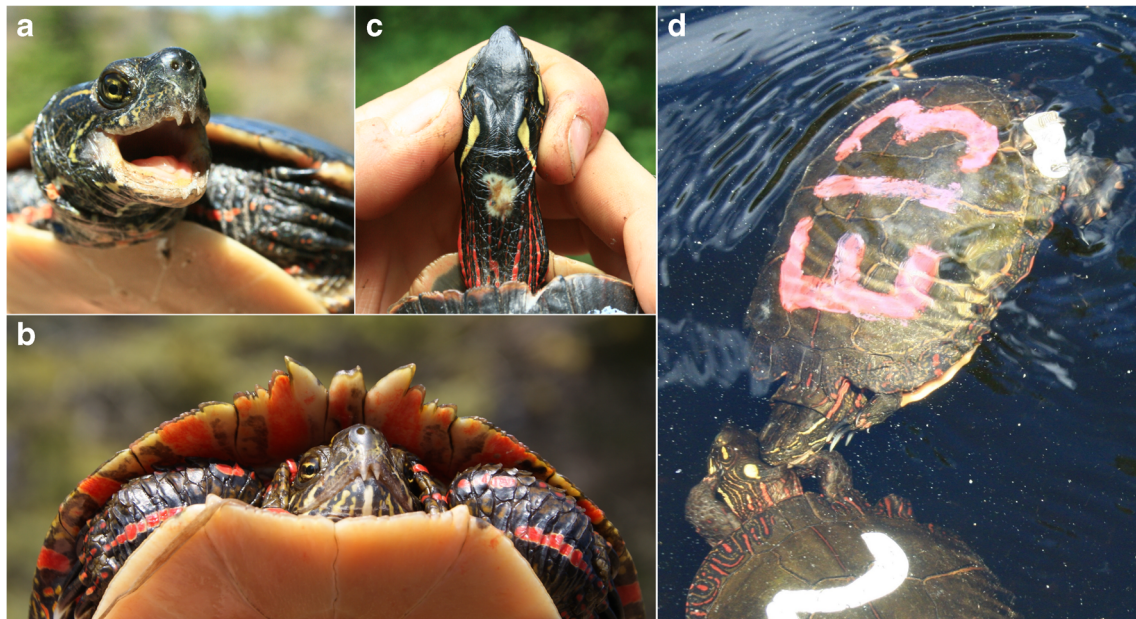


Fig. 1 Sexual weaponry and coercive behavior of male painted turtle (*Chrysemys picta*). **a** Bicuspid sexually size dimorphic tomiodonts (Moldowan et al. 2016a, b) used in biting and restraining females. **b** Projecting and flared anterior carapace (Hawkshaw et al. 2019) used as

a weapon in female coercion. **c** Scarred nape wound of a female. **d** Male E13, member of the long-term study population, biting the nape of a female immediately before initiating shell clattering. Photos a, c, and d by P.D. Moldowan. Photo b by C. LeGros

travel between these wetlands and interact. The sex ratio of the adult population is strongly female-biased (3.44:1, female:male; Samson 2003). A complete site description can be found in Schwarzkopf and Brooks (1985). In early spring, painted turtles were captured by dipnet from canoe and transported and processed in a field laboratory at the Algonquin Wildlife Research Station (AWRS). Midline plastron length (MidPL) was measured using Vernier calipers (to the nearest 0.1 mm). Midline plastron length was recorded as the straight-line measurement extending from between the gular (first plastral) scutes at the anterior to between the anal (sixth plastral) scutes at the posterior (Method H, Iverson and Lewis 2018). Foreclaw and tomiodont length measurements are described in Moldowan et al. (2016b). Individuals are permanently marked with unique carapacial notches (Cagle 1939) and/or shell-mounted aluminum tags (Loncke and Obbard 1972), and a temporary identification code was painted on the shell allowing individuals to be identified from afar and in behavioral trial videos.

Behavioral trials Behavioral trials were conducted in spring (May 14–31, 2013) and late summer (August 15–September 22, 2014) during the two putative breeding periods (Gibbons 1968; Moll 1973; Krawchuk and Brooks 1998; Moldowan et al. 2018). Spring behavioral trials commenced once the body temperature of recently captured basking turtles was $\geq 17^\circ\text{C}$ and surface water temperature reached 15°C , consistent with temperatures during breeding in other wild populations (Ernst 1971), temperatures of maximum ovarian growth and

ovulation in females, and temperatures of testis growth, spermatogenesis, and testosterone secretion in males (Ganzhorn and Licht 1983; Licht and Porter 1985).

Following capture, males were maintained individually in open-top buckets, whereas females were permitted to interact between time of capture and being placed in a trial. Handling time was minimized and did not exceed 15 min (usually < 10 min) from time of capture to placement in a trial. Behavioral trials were conducted in enclosures (183 cm long \times 76 cm wide \times 76 cm deep; adapted from Exo-Terra® Flexarium, full screen terrarium, Rolf C. Hagen Inc., Montreal, Quebec) partially submerged (water depth ~ 60 cm) in situ in the wetlands. The enclosures were constructed of a lightweight PVC pipe frame and fitted nylon mesh walls with an open top, thus permitting water flow and exposure to environmental stimuli (e.g., light, olfactory cues) from the turtles' local habitat. A pole-mounted digital video camera (GoPro®, California, USA) was oriented to provide an overhead view of the trial. One male and three females were placed in each trial, approximating the sex ratio of the study population. Turtles were haphazardly assigned to a trial, although a conscious effort was made to vary female size in each trial. Trials were 2 h in length beginning after the addition of all four turtles into the enclosure. The courtship and reproductive behaviors of wild aquatic turtles are difficult to observe such that complete behavioral sequences are rarely obtained (Liu et al. 2013). We set our trial duration for a time period (i.e., 2 h) that would prioritize animal welfare while still providing ample opportunity for adequate data collection and hypothesis

testing (see ethics statement below). Observers were absent during trials to prevent disturbance that may have altered natural turtle behaviors. Trials were conducted on clear days with low wind between the hours of 1000 and 1600. Within each breeding season (spring or late summer), a male and female were used in a trial only once. A total of 18 complete male-female spring trials (2 h/trial; 36 h) and 28 complete male-female late summer trials were recorded (56 h). A small number of all-male and all-female trials were also conducted to evaluate intrasexual behavior (see [Supplementary Materials](#)).

Ethogram and behavioral trial analysis An ethogram was developed to describe and quantify the reproductive behaviors of painted turtles recorded in the trials (Table S1). Behaviors of male turtles were grouped into three different contexts: neutral interactions (approach, cloacal sniffing), courtship interactions (titillation), and coercive interactions (open-mouth striking, biting, forced submergence, shell clattering). Titillation and open-mouth striking were used as a representative courtship and coercion behavior, respectively (also see [Supplementary Materials](#)). Courtship is defined as non-aggressive male reproductive behavior directed toward a female with no apparent cost to the female. In contrast, sexual coercion involves aggressive male behavior toward females, including the use or threat of force and a resultant cost to the female (Smuts and Smuts 1993). Behaviors resulting from two or more turtles accidentally bumping into each other while in an enclosure corner or swimming along the enclosure walls were excluded from analysis (Thomas 2002). Videos were reviewed and behavioral observations were quantified using the ethogram by both tallying the number of trials demonstrating each behavior and the number of times each behavior was observed in a trial.

To test whether males shift reproductive tactics across ontogeny, we used logistic regression comparing the occurrence (presence/absence) of titillation (representative courtship behavior) and striking (representative coercive behavior) in relation to male body size (MidPL) for the spring and late summer behavioral trials. Also, linear regression was used to test whether male body size (MidPL) was a predictor of the frequency of titillation and striking behavior. To compare the relationship between phenotype and behavior, proportional male foreclaw length and tomiodont length (Moldowan et al. 2016b) were regressed against body size (MidPL) and descriptively compared with data on male behavior (occurrence of courtship and coercion). To minimize observer bias, blinded methods were used when all behavioral data were analyzed. All statistical analyses were completed in R statistical software (R Core Development Team 2019). Findings were considered statistically significant at $\alpha < 0.05$.

Ethics statement Animal use was approved by the Laurentian University Animal Care Committee (AUP #2008-12-02) and

conformed to the Canadian Council on Animal Care guidelines. Research was conducted under permit from Ontario Parks. Maintaining wild-caught turtles in open-air in situ wetland enclosures for 2 h was deemed minimally stressful. As noted above, observers were absent during trials to prevent disturbance. Trials were video recorded and reviewed in full at a later date. Upon video review, we observed male turtles biting and forcibly submerging females. Painted turtles are among the most anoxia tolerant vertebrates, surviving greater than 5 months of submergence while overwintering at cold temperatures, and capable of being submerged at warm temperatures (20–26 °C) for up to 2 days (Herbert and Jackson 1985; Bickler and Buck 2007). Female turtles may have experienced mild hypoxic distress during behavioral trials, a scenario not anticipated at the outset of our study. However, such distress, if experienced, was well within the physiological tolerance of these animals based on experimental research (Herbert and Jackson 1985; Bickler and Buck 2007). No turtles died during the behavioral trials or were in a compromised state following the behavioral trials. All turtles were thoroughly inspected for external wounds, defensive response (recoil into their shell), and general health prior to release. One female received a bite from a male that broke the skin on her nape; the bite was treated with topical antiseptic prior to release. This turtle, as with all other females used in the behavioral trials, have since been recaptured in good health and have been observed nesting in subsequent years of our long-term study.

Results

Behavior occurrence, frequency, and seasonality We evaluated the occurrence (presence/absence) and frequency of male reproductive behaviors. In all trials, males approached, chased, and displayed cloacal sniffing of females irrespective of male body size and season (Table S2). Male biting behavior (17% and 14% of trials) occurred at a frequency comparable to their rate of titillation (11% and 21% of trials) in the spring and late summer, respectively (Table S2). Open-mouth striking was observed in 39% of spring trials and 71% of late summer trials. By contrast, titillation was much less common (Table S2). Compared to the total number of male-female interactions, the proportions of male approach, cloacal sniffing, chasing, and biting were similar in spring and late summer (Table S3). The relative proportion of male courtship behavior (titillation) did not change between spring and summer. The relative proportions of male coercive behaviors (open-mouth striking and shell clattering), increased by approximately 3-fold in late summer compared to spring (Table S3).

In late summer, males aggressively charged toward females, a behavior not seen in the spring (Table S2, S3).

Although rare, the occurrence and frequency of forced submergence and shell clattering greatly increased in the late summer compared to the spring (Table S2, S3). Bite duration was highly variable, from as short as 3 s to nearly 600 s ($N = 16$, mean \pm SD = 128 ± 208 s). Striking and biting were directed at soft tissue of the dorsal, ventral, frontal, and lateral positions of the female's head and neck (Table S5, S6). Males were significantly more likely to engage in shell clattering the longer they bit a female (Logistic regression: $z_{15} = 6.01$, $P < 0.0001$). See [Supplementary Materials](#) for videos and descriptive remarks about coercive male behavior.

Male body size and reproductive behavior Reproductive tactics used by males varied with body size and season. In spring, male body size was not a significant predictor of titillation (logistic regression: $z_{17} = 0.031$, $P = 0.975$, Fig. 2a) or striking (logistic regression: $z_{17} = 1.154$, $P = 0.249$; Fig. 2b); however, in the late summer, small males were marginally significantly more likely to demonstrate titillation (logistic regression: $z_{28} = -1.945$, $P = 0.052$; Fig. 2c), whereas large males were significantly more likely to strike at females (logistic regression: $z_{28} = 2.694$, $P < 0.01$; Fig. 2d). An increase in male body size was associated with a significant decrease in the frequency of titillation in late summer (linear regression: $R^2 = 0.37$,

$t_{27} = -3.96$, $P < 0.0005$; Fig. 3c), but not in spring (linear regression: $R^2 = 0.096$, $t_{16} = 1.31$, $P = 0.21$; Fig. 3a) when titillation was already rare. The frequency of male striking increased significantly with body size in spring (linear regression: $R^2 = 0.36$, $t_{16} = 3.019$, $P < 0.01$; Fig. 3b) and late summer (linear regression: $R^2 = 0.27$, $t_{27} = 3.169$, $P < 0.005$; Fig. 3d).

The mean body size of males (MidPL) demonstrating titillation was 102.2 ± 37.9 mm SD ($N = 7$) and the mean body size of males demonstrating striking was 124.72 ± 24.0 mm SD ($N = 23$; data pooled from spring and summer trials without replicates). At approximately 110 mm MidPL, male behavior appeared to shift from titillation to striking (Figs. 2 and 3); however, there is not a clear dichotomy between behaviors. Combining spring and late summer trials, three males (measuring 102.1, 134.1, and 134.8 mm MidPL), representing 9% of all males tested, demonstrated both titillation and striking (Table S4). Male body size was not related to the total number of male-female interactions in either spring (linear regression: $R^2 = 0.17$, $t_{16} = 1.82$, $P = 0.087$) or late summer (linear regression: $R^2 = 0.027$, $t_{26} = -0.84$, $P = 0.41$), although there was a non-significant trend toward larger males interacting more with females in spring and smaller males interacting more with females in late summer.

Fig. 2 Probability (occurrence) of ontogenetic and seasonal shifts in reproductive tactics of male painted turtles (*Chrysemys picta*). Probability of **a** foreclaw display (courtship behavior; $z_{17} = 0.031$, $P = 0.975$) and **b** open-mouth striking (coercive behavior; $z_{17} = 1.154$, $P = 0.249$) relative to male body size during spring behavioral trials. Probability of **c** foreclaw display ($z_{28} = -1.945$, $P = 0.052$) and **d** open-mouth striking ($z_{28} = 2.694$, $P < 0.01$) relative to male body size during late summer behavior trials. Solid line = best fit of logistic regression model; dashed line = standard error estimates

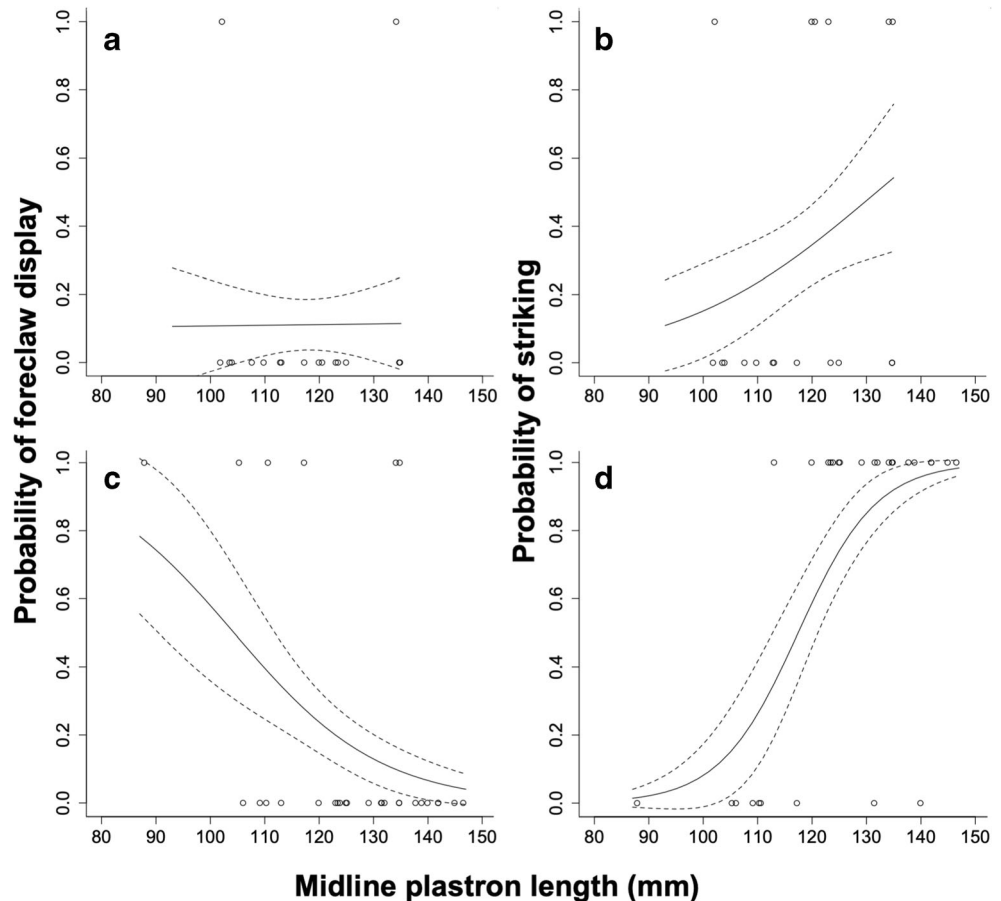
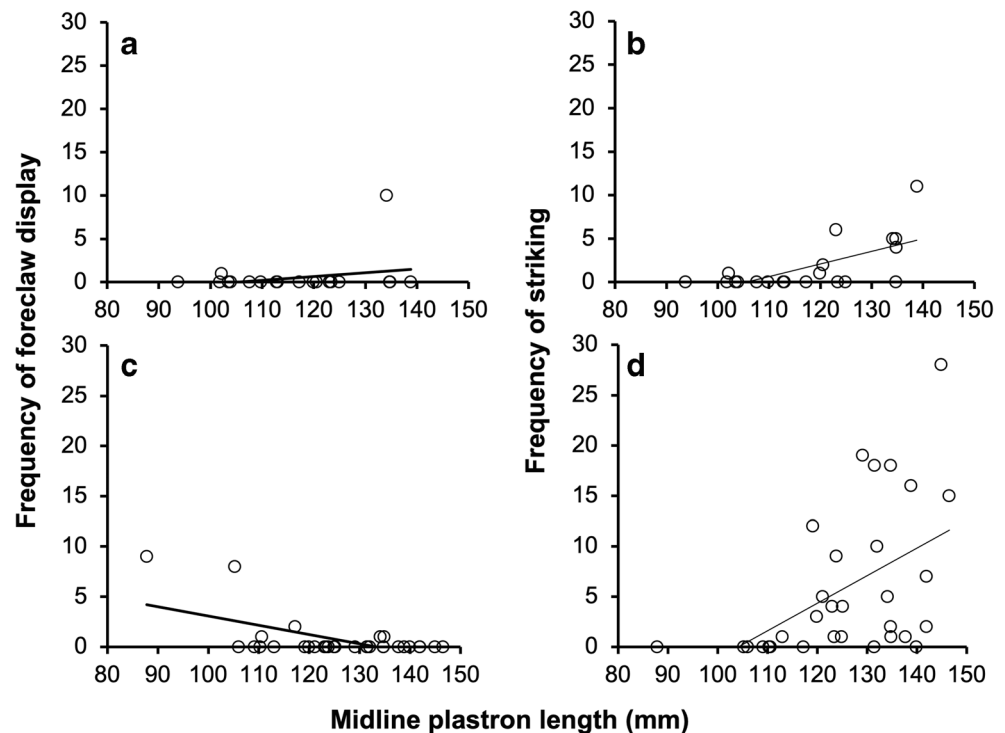


Fig. 3 Frequency of ontogenetic and seasonal shifts in reproductive tactics of male painted turtles (*Chrysemys picta*). Frequency of **a** foreclaw display (courtship behavior; $R^2 = 0.096$, $t_{16} = 1.31$, $P = 0.21$) and **b** open-mouth striking (coercive behavior; $R^2 = 0.36$, $t_{16} = 3.019$, $P < 0.01$) relative to male body size during spring behavioral trials. Frequency of **c** foreclaw display ($R^2 = 0.37$, $t_{27} = -3.96$, $P < 0.0005$) and **d** open-mouth striking ($R^2 = 0.27$, $t_{27} = 3.169$, $P < 0.005$) relative to male body size during late summer behavior trials



Phenotype-behavior matching Male painted turtles used their foreclaws as putative ornaments for courtship display and their tomiodonts as weapons for coercion. The proportional size of the foreclaws significantly decreased with body size (linear regression: $R^2 = 0.35$, $t_{68} = -6.00$, $P < 0.0001$), whereas the proportional size of the tomiodonts significantly increased with body size (linear regression: $R^2 = 0.17$, $t_{68} = 3.72$, $P < 0.001$; Fig. 4). This ontogenetic change in morphology coincides with the ontogenetic shift in reproductive tactics from courtship to coercion (Figs. 2 and 3).

Discussion

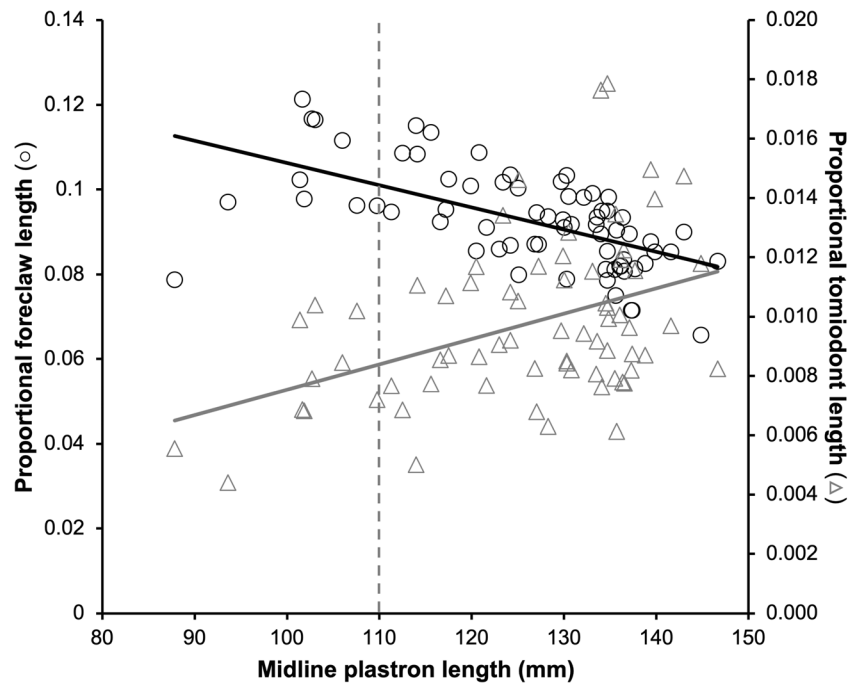
We found that male painted turtles used coercive reproductive behaviors supported by sexual weapons (tomiodonts and a serrated anterior carapace), and that male phenotype matches reproductive tactics that switch across ontogeny. Small males invested in courtship behavior (titillation) and structures (foreclaws), and larger males invested in coercive behaviors (chasing, open-mouth striking, biting, forced submergence, and shell clattering) and sexual weapons.

Ontogenetic shift in reproductive behavior Morphological and/or behavioral traits that form the basis of alternative reproductive tactics typically have a dichotomous distribution and individuals allocate resources to one alternative or the other (Brockmann 2001; Taborsky et al. 2008). In our painted turtles, some males across a range of (larger) body sizes

demonstrated both titillation and striking, although there was a threshold body size (110 mm MidPL) at which reproductive tactics appeared to shift (Figs. 3 and 4, Table S4). Others studying the reproductive tactics of emydid turtles have also reported a shift in reproductive behaviors with male size. For example, small male cooters (*Pseudemys nelsoni*) performed titillation, whereas larger males were prone to biting and aggression toward females (Lardie 1983; Kramer 1986, 1989; see Moldowan 2020). Similarly, male sliders (*Trachemys scripta*) show size-dependent alternative mating tactics; larger males have a much higher precopulatory display rate coupled with chasing and biting relative to the low precopulatory display rate and titillation courtship of smaller males (Thomas 2002). Body size is a significant predictor of biting propensity in juvenile, adult female, and adult male *T. scripta* (Hites et al. 2013).

Biting during reproduction is thought to be an evolutionarily conserved behavior of Testudines (Jackson and Davis 1972; Liu et al. 2013). Biting can be an important means of immobilizing a female for breeding (Auffenberg 1966; Jackson and Davis 1972; Sacchi et al. 2003; Liu et al. 2013), and may be of particular importance in highly mobile, fully aquatic species. Biting may also serve in female arousal (Kramer 1986; Comuzzie and Owens 1990) or as a tactile stimulus (Liu et al. 2013). Chasing and biting may also drive females to preferred breeding locations, such as shallow water (Ernst and Barbour 1972; Harding and Bloomer 1979; Kauffman 1992). Aggressive tactics may serve as an indicator of male strength and/or affirm social dominance. Social

Fig. 4 Reproductive phenotype shift across ontogeny in male painted turtles (*Chrysemys picta*). Male foreclaws, putative ornaments used in courtship, exhibit a decrease in size relative to body size (midline plastron length), whereas the tomiodonts, weaponry used in sexual coercion, increase in relative size when compared to male body size. This shift in phenotype matches the observed transition in reproductive tactics from courtship to coercion across ontogeny in the painted turtle (approximately 110 mm midline plastron length; vertical dashed line)



hierarchy may be present in painted turtles based on limited observations of dominance in captive settings (Ernst and Lovich 2009), aggressive interactions between basking individuals (Bury et al. 1979), and conspecific wounding (Moldowan et al. 2020).

Males that exhibit coercive tactics potentially have a lot to gain, even from a single copulation. The widespread ability of female turtles, the painted turtle included, to store sperm for several years can secure a male's paternity for multiple clutches (Pearse et al. 2002; McGuire et al. 2014). Larger females have a higher fecundity (MacCulloch and Weller 1998; Congdon and van Loben Sels 1991, 1993; Rollinson and Brooks 2008b) and larger females disproportionately bear wounds (Moldowan et al. 2020), suggesting that male coercive tactics serve to maximize reproductive success.

Sexual weaponry in Testudines In a thorough treatment of animal weaponry by Emlen (2008), examples of testudine weaponry were conspicuously absent. The anterior plastron of males of some tortoise species (e.g., *Astrochelys yniphora*, *Centrochelys sulcata*, *Chersina angulata*, *Gopherus* spp.) is modified into a weapon used in male-male contests and female harassment (Tuma 2016; Hawkshaw et al. 2019). The highly serrated and projecting anterior carapace (upper shell) of male painted turtles is one of the few described examples of sexual weaponry in a freshwater turtle species (Fig. 1b; Hawkshaw et al. 2019; also see the spine-tipped tail of kinosternid turtles, Berry and Shine 1980). Our study is the first report of shell clattering in painted turtles and only the second for an aquatic turtle species. Kramer (1984, 1989) coined the term shell clattering based on observations of male

biting, forceful contact of the male and female shell, and audible knocking in *Pseudemys nelsoni*. Among Testudines, the use of the shell as a sexual weapon by males has also been termed shell ramming and shell clapping (Liu et al. 2013), particularly for terrestrial species. Male box turtles (*Terrapene* spp.) are reported to make lunging bites and deliver repeated blows to females with their shell (Brumwell 1940; Evans 1953, 1968). In the marginated tortoise (*Testudo marginata*), male mounting success is highly correlated with the number of bites and rams given to females (Sacchi et al. 2003). Bouts of shell contact can be forceful enough to produce loud sound (Brown 1974; Kramer 1984, 1989; Video S1, S2), audible up to 100 m away in large tortoises (Auffenberg 1977). Males may physically displace females during bouts of coercion by dragging or ramming (Evans 1953; Auffenberg 1977; Kramer 1986; Video S1, S2, S3). Given the evolutionary (intrafamily) relatedness of *Chrysemys* and *Pseudemys* (Seidel and Smith 1986; Stephens and Wiens 2003, 2009) as well as shared reproductive behaviors with other members of Emydidae (e.g., titillation in *Chrysemys*, *Pseudemys*, *Trachemys*, *Graptemys*; Seidel 2002; Stephens and Wiens 2003; Ernst and Lovich 2009), shell clattering may be a widespread coercive reproductive behavior that has been overlooked.

Phenotype-behavior matching: courtship ornaments and coercive weapons The ontogenetic shift in investment from foreclaws to tomiodonts (Fig. 4; and shell weaponization, Hawkshaw et al. 2019) coincides with a shift in reproductive behavior from courtship to coercion (Figs. 1, 2, and 3). Given that turtles are long-lived, we hypothesize that these shifts in

trait investment and behavior maximize male reproductive success. Male painted turtles in our population mature on average at 90 mm MidPL (range 85–95 mm MidPL), at approximately 8 years of age (range 7–10 years; Samson 2003). Males demonstrated a shift in reproductive tactics from titillation to striking behavior at approximately 110 mm MidPL (Figs. 2 and 3), which would occur at an estimated age of 15 years (95% CI: range 12 to 20 years; Samson 2003; M.G. Keevil, unpublished data). Painted turtle lifespan can exceed 60 years (COSEWIC 2018; unpublished data from long-term Algonquin Park study). Given that reproductive senescence has not been detected (although focussed on females; Congdon et al. 2003; Keevil 2020) and assuming a full lifespan, it is possible that a greater portion of the male reproductive lifespan is spent demonstrating coercive tactics rather than courtship.

We observed male titillation behavior infrequently and mostly restricted to smaller males. Growth of the foreclaws in emydids is a testosterone-mediated process (Evans 1946, 1951, 1952). Foreclaw elongation occurs rapidly at sexual maturity then claw growth is slow or non-existent post-maturity (Gibbons 1968; Gibbons and Greene 1990; Frazer et al. 1993; Moldowan et al. 2016b). Relative to body size, small males have proportionately longer foreclaws than large males (Fig. 4). Consistent with findings in *Trachemys* (Thomas 2002), the reduced investment in foreclaw growth (Fig. 4) and the declining use of titillation with size (Figs. 2 and 3) calls into question the functional role of titillation. Although titillation is a regularly observed behavior in emydid (Deirochelyinae) courtship, the other contexts in which this behavior occurs strongly suggests that it is not solely related to reproduction (Hearlson 2011). Thomas and Altig (2006) make the distinction between titillation and foreclaw display stating that the former should be reserved as a description of reproductive behavior and the latter represents a non-reproductive communicative behavior (Table S1). Others have suggested that foreclaw display may function in species or individual recognition (Jackson and Davis 1972; Kramer 1989; Kramer and Burghardt 1998), as a reproductive isolating mechanism (Jackson and Davis 1972), in information gathering about novel objects (Cagle 1955), in the establishment and maintenance of social dominance (Rives 1978), in precocious courtship and play (Kramer and Burghardt 1998), and/or as a form of subtle sexual coercion (R. Shine, personal communication; see Supplementary Materials).

Consistent with theory about animal weaponry (Emlen 2008), the largest male painted turtles have the largest and most prominent tomiodonts (Moldowan et al. 2016b) and shell weaponry (Hawkshaw et al. 2019). Although the selective pressures leading to the evolution of the sexually dimorphic tomiodonts (Moldowan et al. 2016a, b) and anterior carapace of male painted turtles (Hawkshaw et al. 2019) are uncertain, the weight of current evidence suggests a sexual

selection hypothesis (Moldowan et al. 2016b), as opposed to ecological (e.g., trophic dimorphism) and/or intrasexual (e.g., from male-male competition; Rico-Guevara and Hurme 2019) selective pressures. Although it appears that male weaponry is primarily used for female antagonism and acquiescence, male-male competition has been inferred. Male-male aggression has not been observed in situ but males demonstrate wounding consistent with that of females, albeit at a much lower frequency (Moldowan et al. 2020; also see Supplementary Materials for notes on all-male behavioral trials).

Female wounding and cost Male aggression is potentially costly for females. Males directed striking and biting around the soft tissue of the head and neck of females (Fig. 1, Table S5, S6), consistent with the wounding patterns observed in females of our study population and in species that demonstrate sexually coercive mating systems (Moldowan et al. 2020). Most bite durations were short (< 30 s), although some periods of biting and forced submergence approached 10 min in duration (Table S6). Painted turtles are reputed for their ability to tolerate extreme periods of oxygen deprivation, particularly at cold overwintering temperatures (Herbert and Jackson 1985; Bickler and Buck 2007). Under late summer conditions, the combination of rigorous struggling, high water temperatures, and high female metabolism from follicular development (Congdon and Tinkle 1982; Mitchell 1985; Rollinson and Brooks 2008a, b; Rollinson et al. 2012) could reasonably induce hypoxia in submerged females (Glass et al. 1983; Herbert and Jackson 1985). Males using coercive tactics such as biting and submergence may force females into a cost trade-off: to breathe or breed. If the costs of remaining submerged (e.g., hypoxia, drowning) are greater than the costs of mating, a female may acquiesce and allow a male to copulate. However, female resistance may outlast or dislodge a biting male, or males may be forced to release their bite and surface because of oxygen limitation. Coercion could drive females away from optimal foraging areas, reduce their time available for necessary activities (e.g., feeding, basking), and divert energy into healing and immune response to combat infection in wounds from bites. Harassment and healing may be particularly costly in our northern study population because of thermal and energetic constraints (Koper and Brooks 2000; Rollinson and Brooks 2007, 2008b).

Evolution of coercion in the emydid mating system The elongate foreclaws and titillation courtship display of some male emydid taxa (Deirochelyinae) are derived reproductive characters, having hypothetically evolved to assist in female acquiescence and to supersede ancestral biting tactics during courtship (Jackson and Davis 1972; Liu et al. 2013). If male aggression is costly to females, we would expect that females demonstrate a preference for non-aggressive titillation courtship display. Given that smaller males demonstrate

proportionately more exaggerated ornaments (foreclaws; Fig. 4), we expect that smaller males would be best able to exploit female preference. As a result, small males are expected to be highly competitive compared to larger, proportionately less ornamented, males when courting females. As males “grow into” their foreclaws, they may experience a decline in attractiveness to females. Thus, an ontogenetic shift in male reproductive tactics from courtship to coercion is expected, especially over the long male reproductive lifespan. If larger males experience a decline in reproductive success because females find them less attractive, large males instead adopt coercive reproductive tactics to circumvent female choice in an attempt to remain reproductively competitive. An alternate scenario in which runaway sexual selection promotes increasing exaggeration of the foreclaws (in response to female preference) is plausible but not observed, perhaps because of costs borne by males with this trait (e.g., inhibited locomotion, vulnerability to predation).

Reproductive tactics in relation to population density, sex ratio, and seasonality Environmental conditions, such as population density and operational sex ratio (Andersson 1994), influence mating system dynamics. Mate competition is expected to intensify with increasing population density and male-biased sex ratios (Krupa and Sih 1993; Rowe et al. 1994; Cureton et al. 2010; Székeley et al. 2014). In addition, operational sex ratio is a strong driver of mating behavior because it dictates the intensity of intrasexual competition and mating opportunity (Clutton-Brock and Parker 1992; Kvamemo and Ahnesjö 1996). In water strider (*Gerris* spp.) mating systems, a male-biased sex ratio is associated with a greater per capita harassment rate of females, decreased female mating resistance, and an increase in the probability of male mating, mating frequency, and mating duration (Clark 1988; Arnqvist 1992; Rowe 1992; Krupa and Sih 1993; Rowe et al. 1994; Weigensberg and Fairbairn 1994). Work on tortoises has demonstrated that high population density and male-biased populations can elevate the frequency and severity of female wounding and that male coercion may be maladaptive under these conditions (Golubović et al. 2018).

Our population density estimates are low to intermediate, and our sex ratio is strongly female-biased (see Methods) compared to estimates reported from other populations (Ernst and Lovich 2009; COSEWIC 2018). Therefore, given an absence of aberrant demographic parameters in our study population, we suspect that sexual coercion is widespread yet underreported in this common and well-studied species. Preliminary data from sampled museum collections (PDM unpublished data) as well as geographically widespread and demographically different study populations (e.g., E.S. George Reserve, Michigan, JD Congdon; Wascania Marsh, Saskatchewan, K Marchand) have provided preliminary evidence of female wounding and coercive behavior.

Capture data (Moldowan et al. 2018) and the results of behavioral trials suggest that late summer is the primary breeding season for our northern population of painted turtles. Males in our study population maintain activity later into autumn (Moldowan et al. 2018), extending the length of their active season and potentially increasing mate-searching activities (Morreale et al. 1984; Thomas et al. 1999). Although spring is purported to be the primary breeding season for *Chrysemys* (Gibbons 1968; Ernst and Lovich 2009), reproductive physiology studies have shown heightened sperm production and presence of sperm in the female reproductive tract in late summer and early autumn (Ernst and Lovich 2009). The understudied late summer breeding period may explain why coercive behavior has not been previously reported.

Study limitations We were unable to confirm whether the coercive behavior of male painted turtles resulted in forced copulation. The 2-h trial period may not have been long enough to observe copulation. Pre-copulatory pursuit and courtship by male emydids is lengthy (Jackson and Davis 1972), lasting hours to days (Kramer 1989; Kramer and Fritz 1989), and potentially even weeks (Ernst 1971). Despite extensive observations of reproductive behavior (~150 h, Kramer 1989; 96 h, Hearlson 2011), others have not observed copulation in captive or wild emydids. Although coercive male behavior did not result in immediate copulation, harassment and intimidation can function to increase female sexual co-operation in the future (Goodall 1986; Smuts and Smuts 1993; Andersson and Iwasa 1996). Future researchers may wish to extend the length of the behavioral trial period.

We performed a small number of intrasexual trials, the results of which provide limited information about male-male and female-female interactions (Supplementary Material). Additional intrasexual behavioral trials would complement the detailed intersexual trials presented herein. Females rarely demonstrated aggression toward each other, but males displayed intrasexual aggression and conspecific wounding (Moldowan et al. 2020). It is possible that dominance hierarchies exist, as has been reported for wood turtles (*Glyptemys insculpta*, Emydidae; Kauffman 1992) and several tortoise species (Testudinidae; Auffenberg 1977; Berry 1986; Mann et al. 2006).

Finally, our study indirectly tested an ontogenetic shift in reproductive tactics by sampling individuals across a body size gradient. A direct test of shifts in reproductive tactics by conducting behavioral trials across an animal's lifetime would be ideal. However, the slow growth and longevity of turtles does not make this feasible. Sampling individuals across a gradient of known ages (rather than simply sizes) would be ideal to assess ontogenetic shifts.

Future research and concluding remarks In painted turtles, small males have proportionately long ornamental

foreclaws used for display, whereas large males have large tomiodonts, a weaponized shell, and demonstrate coercive behaviors including striking, biting, forced submergence, and shell clattering. We wish to highlight the importance of conducting behavioral trials with wild individuals in their native habitats while subject to natural cues. Future research should address paternity to assess whether tactic switching improves a male's reproductive success. Also, conducting hormone (testosterone) assays across the active season, life stages, and sexes would be useful as a possible mechanism relating morphology, behavior, and seasonality of reproduction. Assessing the relationship between male morphology (e.g., tomiodont size) and performance (e.g., bite force) would further contribute to addressing questions related to phenotype-behavior matching.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Animal handling was approved by the Laurentian University Animal Care Committee (AUP #2008-12-02) and conforms to the guidelines of Canadian Council on Animal Care.

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