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

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 (

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. (2016). Individuals are permanently marked with unique carapacial notches (Cagle

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).

Although rare, the occurrence and frequency of forced submergence and shell clattering greatly increased in the late summer compared to the spring (Table S3). Bite duration was highly variable, from as short as 3 s to nearly 600 s (

Phenotype-behavior matching

Male painted turtles used their foreclaws as putative ornaments for courtship display and

hierarchy may be present in painted turtles based on limited observations of dominance in captive settings (Ernst and Lovich 2009

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 (Ewert 1946; Wilson 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 1). 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 (Rivers 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

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 expect-

Herbert CV, Jackson DC (1985) Temperature effects on the responses to prolonged submergence in the turtle Chrysemys picta bellii. II. Metabolic rate, blood acid-base and ionic changes, and cardiovascular function in aerated and anoxic water. Physiol Zool 58:667–680

Hites R, Caddell G, Stone MB, Stone PA (2013) Relationships of body size and male melanism to biting propensity in red-eared sliders (Trachemys scripta). Herpetol Rev 44:446–449

Iverson JB, Lewis EL (2018) How to measure a turtle. Herpetol Rev 49: 453–460

Jackson CG, Davis JD (1972) A quantitative study of the courtship display of the red-eared turtle, Chrysemys scripta elegans (Wied). Herpetologica 28:58–64

Kauffman JH (1992) The social behavior of wood turtles, Clemmys insculpta, in Central Pennsylvania. Herpetol Monogr 6:1–25

Keevil MG (2020) Joint estimation of growth and survival from mark-recapture data to improve estimate of senescence in wild populations: comment. Ecology e03232. https://doi.org/10.1002/ecy.3232

Keevil MG, Brooks RJ, Litzgus JD (2017) Patterns of interspecific aggression inferred from injuries in an aquatic turtle with male-biased