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ORIGINAL ARTICLE

Basking buddies: factors influencing social associations in basking aggregations of turtles

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Abstract

Basking in groups with conspecifics is extensively documented in reptiles, and in some clades, notably Scincidae, basking aggregations can be representative of repeatable and stable social kin groups. Evidence for social basking in non-squamate reptiles is less reported, but mounting evidence suggests that social behaviour in turtles may be common. To elucidate the social drivers of basking aggregations, we recorded basking behaviour in a population of Midland Painted Turtles (*Chrysemys picta marginata*) over two active seasons. We explored potential factors influencing associations during basking aggregations, and tested whether social basking is impacted by individual traits that may reflect dominance hierarchies. We used network analysis to construct matrices of social association between basking individuals, and explored spatial overlap, genetic relatedness, body size, and sex as possible predictors of these population-level associations. We also quantified individual social behaviour by calculating network metrics and examined whether body size and a proxy of boldness influenced individual-level social behaviour. We found no support for spatial overlap, kinship, body size, or sex similarity as drivers of social associations while basking. Turtles did not generally associate with one another, but when they did, close to the majority of association were preferred (i.e., non-random). Further, we found that body size and a proxy of boldness affected the social behaviour of female turtles. These individual-level findings suggest that a dominance hierarchy may influence social structure in basking aggregations of Painted Turtles. Our findings have implications for understanding the evolution of cryptic sociality, and call for more thorough examination of social organization in a wider range of non-avian reptiles.

Significance statement

The dynamics of animal aggregations in many taxa remain understudied. We explored factors driving basking aggregations of freshwater turtles and how individual characteristics may influence social interactions. We found that common drivers of sociality, like spatial overlap and kinship, did not influence basking aggregations of turtles at our study site. However, individual traits, specifically body size and boldness, impacted social interactions of females during basking, suggesting that a dominance hierarchy may guide shared use of basking sites. Such hierarchies are common social structures in species that associate in non-kin groups.

Keywords Chelonian · Conspecific grouping · Reptile · Social behaviour · Sociality

Introduction

Sociality can be defined as the degree to which individuals in a population aggregate together and interact (Gromov 2013; Hofmann 2014). Tendencies to aggregate vary greatly among taxa: animals can be solitary where interactions with conspecifics occur only during territory disputes or mating (Ward and Webster 2016), aggregations may be restricted to reproductive events or overwintering periods (Graves and Duvall 1995), or animals may live in kin-based cooperative

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groups or complex eusocial societies (Kappeler and van Schaik 2002; Nowak et al. 2010). A variety of factors may explain this variation among taxa in their tendency to aggregate. For instance, animal aggregations may be caused by environmental constraints (termed 'the ecological constraints hypothesis', 'habitat heterogeneity hypothesis' and/or the 'socioecological approach'; Lindenmayer and Fischer 2006; While et al. 2009; Michael et al. 2010; Nowak et al. 2010; Gromov 2013), where animals group together when required resources (food, shelter or basking sites, overwintering habitat, oviposition or gestation sites, or mates) are spatiotemporally constrained (Graves and Duvall 1995; Hatchwell and Komdeur 2000). Life history characteristics may also increase a species' tendency to aggregate (Covas and Griesser 2007; Blumstein and Møller 2008; Ward and Webster 2016); for example, it has been found that species with greater longevity, later age at maturity, and that are viviparous are more likely to exhibit social tolerance towards conspecifics. Thus, both life-history and ecological factors can be predictors of an animal's social tendencies.

There are fitness costs and benefits to participating in aggregations. Costs of group-living include an increased conspicuousness to predators, and exposure to disease and parasites (Alexander 1974; Chapple 2003; Lanham and Bull 2004; Clark et al. 2012; Ebensperger et al. 2012). Benefits include enhanced vigilance against predators (i.e., the 'many eyes' hypothesis; Caraco et al. 1980) and increased access to resources (Chapple 2003; Lanham and Bull 2004; Clark et al. 2012; Ebensperger et al. 2012). When benefits outweigh costs, aggregations may be maintained over the long-term (i.e., formation of stable social groups) and lead to development of more complex forms of sociality (Ebensperger et al. 2012; Ward and Webster 2016). Furthermore, if groups consist of kin, there may also be indirect fitness benefits associated with aggregation (Hamilton 1964a, b; Taylor 1992a, b). Kin selection and kin recognition can facilitate maintenance of stable social systems (Hamilton 1964a, b; Ho et al. 2013) and provide the basis for the evolution of complex social behaviours like cooperation and altruism (Clutton-Brock 2002). Thus, in addition to environment and life-history, genetic relationships between individuals should be considered when investigating the dynamics of animal aggregations.

Basking has long been recognized as a critical component of the ecophysiology of ectothermic animals like non-avian reptiles (hereafter referred to as reptiles). Basking is central to thermoregulation (Schwarzkopf and Brooks 1985; Carrière et al. 2008; Bulté and Blouin-Demers 2010a; Sears et al. 2016), but also has non-thermoregulatory functions (reviewed in Congdon 1989), including digestion (Harwood 1979; Hennemann 1979; Sturbaum 1982; Chessman 1987; Hammond et al. 1988), removal of external parasites and growths (Cagle 1950; Neill and Allen 1954; Boyer 1965; Ryan and Lambert 2005), vitamin D synthesis (Moll and Legler 1971; Ferguson et al. 2003; Peterman and Ryan 2009), immune function (Monagas and Gatten 1983), and reproduction (Congdon and Tinkle 1982; Whittow and Balasz 1982; Schwarzkopf and Shine 1991; Wapstra 2000; Bulté and Blouin-Demers 2010b). Many reptiles bask in aggregations, which may have a social function beyond simple tolerance of conspecifics (Réale et al. 2007). In some instances, group basking is hypothesized to occur as a result of limited suitable basking habitat (Bury and Wolfheim 1973; Lindeman 1999), which has been invoked to explain patterns of association in two communally-basking cordylid lizards (*Cordylus macropholis* and *Karusasaurus polyzonus*; Visagie et al. 2005). However, basking aggregations may occur for reasons independent of limited basking habitat, as a diversity of social systems in reptiles have been described by studying conspecific interactions within basking aggregations (O'Connor and Shine 2004; Shine et al. 2004; Clark et al. 2012; Watson et al. 2020; Riley et al. 2021).

Among reptiles, sociality is most thoroughly documented in squamates (reviewed in Gardner et al. 2016; Bull et al. 2017), but our understanding of sociality and social basking in other reptilian orders is less well developed, in particularly in Testudines (Doody et al. 2013; Wilkinson et al. 2025). Turtles often aggregate during mating and nesting (as reviewed in Graves and Duvall 1995), while foraging (Green Sea Turtle, *Chelonia mydas*: Thompson et al. 2015; Suwannee Cooters, *Pseudemys concinna suwanniensis*: Adler et al. 2018), overwintering (as reviewed in Ultsch 2006), and basking. Many emydid turtles are often seen in inter- and intra-specific basking aggregations (e.g., Cagle 1950; Boyer 1965; Schwarzkopf and Brooks 1985; Lindeman 1999), and a number of turtle species are noted to be tolerant of sharing a basking structure with conspecifics (Eastern Box Turtle, *Terrapene carolina carolina*: Dolbeer 1969; Madden 1975; Coahuilan box turtle, *Terrapene coahuila*: Brown 1974; Northern Map Turtle, *Graptemys geographica*: Flaherty and Bider 1984; Wood Turtle, *Glyptemys insculpta*: Kaufmann 1992). Yet, these aggregations have typically been viewed through the lens of environmental constraints, where aggregations occur simply because suitable basking areas are limited (Lindeman 1999). Yet, social behaviour may also underlie basking aggregations, although careful analyses that disentangle environmental constraints from social behaviour are lacking. While turtles are a taxon often categorised as "asocial", there are several reports of social behaviour in this group (Kaufmann 1992; Rife 2007; Wilkinson et al. 2010; Masin et al. 2020; Kell et al. 2021). Further, the bet-hedging life history strategy exhibited by turtles (e.g., long-lived, late maturation, high adult survival; Ernst and Lovich 2009) may predispose them to sociality (Covas and Griesser 2007; Blumstein and Møller 2008; Ward and Webster 2016).

Some chelonians exhibit behaviours that are suggestive of complex sociality (Guyer et al. 2014; Kell et al. 2021; Wilkinson et al. 2025). Turtles exhibit gaze following (Red-footed Tortoise, *Chelonoidis carbonaria*; Wilkinson et al. 2010); the ability to align gaze direction with a conspecific, which is posited to reflect use of social information. There is also evidence that juvenile Painted Turtles (*Chrysemys picta*) navigate using social information, specifically ultraviolet cues from the sloughed skin and faeces of adults (Roth et al. 2015). Turtles display social learning (i.e., individuals gain new information by observing behaviour of conspecifics; Wilkinson et al. 2010; Davis and Burghardt 2011; Webster 2023) and dominance hierarchies that are mediated by an individual's behaviour and size (Desert Tortoise, *Gopherus agassizii*: Berry 1986; Wood Turtle, Kaufmann 1992; Angulate Tortoise, *Chersina angulata*: Mann et al. 2006; European Pond Turtle, *Emys orbicularis galloitalica*: Masin et al. 2020; Painted Turtle: Koprowski et al. 2024), which suggests organization in their social structure. Further, at least ten species of turtles, including marine (Ferrara et al. 2014a, b, c; 2019; McKenna et al. 2019) and freshwater (Giles et al. 2009; Geller and Casper 2020; Lacroix et al. 2022) species, are capable of vocal communication with conspecifics. Our understanding of the function of these calls is still limited, but they appear to play a role in eliciting parental care (Ferrara et al. 2014a) or coordinating nest-emergence behaviour (Lacroix et al. 2022; but see McKenna et al. 2019). Based on *ex situ* experiments, there is contrasting support for whether kinship effects interactions. In juvenile Eastern Box Turtles, social interactions were not biased towards/away from kin (Tetzlaff et al. 2022), whereas juvenile Northern Diamondback Terrapins (*Malaclemys terrapin terrapin*) were more willing to bask with kin, and kinship affected whether interactions were aggressive (Rife 2007). Overall, current literature on social behaviour in turtles suggest that further study, particularly in wild populations, is necessary to understand the diversity and function of observed social behaviour.

Painted Turtles are one of the most well-studied of all emydid turtles in North America (Lovich and Ennen 2013), and their tendency to bask in groups is well known (e.g., Lindeman 1999; Ernst and Lovich 2009; Fenech 2023). Previous research based on observations of dominance in captive settings suggests that a social hierarchy may be present in Painted Turtles, and that personality traits may facilitate formation of hierarchies (Ernst and Lovich 2009; Koprowski et al. 2024). Painted Turtles may also act aggressively toward conspecifics while basking (Bury and Wolfheim 1973), and alternative reproductive tactics are expressed based on male size (Moldowan et al. 2020). However, there has been limited investigation into social factors that might influence tendency to aggregate while basking in Painted Turtles. Here, we explore factors driving association in Painted Turtles while basking, including examination of individual space-use, kinship, morphology, and demography. The objectives of our study were: (1) to quantify population-level social associations of Painted Turtles during basking and investigate the factors driving them, and (2) investigate factors that impact the social behaviour of individual turtles during basking. Ours is the first study to examine drivers of Painted Turtle social associations and behaviour while basking in a wild population.

Methods

Study site and population

We studied a population of approximately 225 (128 turtles/ha; M. Keevil and S. Sanders, unpubl. data) Midland Painted Turtles (*Chrysemys picta marginata*, hereafter referred to as Painted Turtles) living in Wolf Howl Pond, a wetland in Algonquin Provincial Park (45°34' N, 78°41' W). Turtles at this site have been studied since 1978, and this population size estimate is based upon 42 years of mark-recapture data (R. Brooks et al., unpubl. data; Samson 2003). Anecdotally, turtles in Wolf Howl Pond tend to stay in the same area year-to-year, but natural environmental variation (e.g., flooding events creating new habitat) can present opportunities for movement into areas of lower conspecific density (NR, pers. obs.). More broadly, Midland Painted Turtles tend to move 68–97 m/day (Rowe et al. 2003; Rowe and Dalgarn 2010; Jaeger and Cobb 2012) and have home ranges that vary in size from 1.2 to 2.9 ha (Rowe et al. 2003; Rowe and Dalgarn 2010). Wolf Howl Pond is a 1.7 ha Black Spruce (*Picea mariana*) bog containing partially submerged logs and floating mats of Sphagnum (*Sphagnum* spp.) used by turtles for basking, Bladderwort (*Utricularia vulgaris*), Bog Leatherleaf (*Chamaedaphne calyculata*), Marsh Spike-Rush (*Eleocharis smallii*), and White Beakrush (*Rhynchospora alba*).

The Painted Turtles in Wolf Howl Pond each have a unique numeric or alphanumeric identity. These identities are based on one of three forms of marking: (i) marginal scute notch codes (based on Cagle 1939), (ii) aluminum ID tags affixed to posterior marginal scutes (described for Snapping Turtles, *C. serpentina,* by Loncke and Obbard 1977), and (iii) passive integrated transponder (PIT) tags implanted into a turtle's right posterior inguinal space (Smyth and Nebel 2013). For our study, turtles were captured by dip net or hand from canoes in April and May of 2019 and 2020, and transported to the Algonquin Wildlife Research Station to collect morphometric data and visually-mark each individual. Midline carapace length (midCL) was measured with digital Vernier calipers to the closest 0.01 cm. All turtles had their unique identities painted on their carapace using TREMCLAD®

oil-based paint to allow for field identification at a distance with binoculars. These paint markings are lost when turtles annually shed their scutes, but remained on all turtles during observations of their basking behaviour.

Basking surveys

In general, turtles are frequent atmospheric (i.e., terrestrial) and aquatic baskers (Lovich 1990; Lefevre and Brooks 1995; Lindeman 1999; Cadi and Joly 2003; Dubois et al. 2009). Turtles atmospherically bask on a wide range of substrates, most notably fallen logs and vegetation mats that allow them to fully remove themselves from water (Boyer 1965; Moll and Legler 1971; Lindeman 1999; Peterman and Ryan 2009). These types of basking behaviours are also observed in Painted Turtles at Wolf Howl Pond. In our study, basking surveys began each season when turtles in Wolf Howl Pond had been exhaustively sampled. An exhaustive sample was defined as approximately 180 turtles being captured (90% of the estimated population), processed for data collection as per the protocol for the long-term study (Samson 2003), and released to their location of capture. In 2019, 40 basking surveys were carried out from 24 May to 18 June. In 2020, 39 basking surveys were carried out from 17 May to 8 June. During these periods, two surveys were conducted daily, at 1000 h and 1600 h. CJR led these surveys in both years with the aid of a field technician that differed between years. During surveys, the pond was visually scanned from its perimeter using binoculars, and then from a distance of 1–5 m in a canoe by a pair of researchers. Surveys lasted approximately one hour, and researchers left the site immediately after completing morning surveys, and did not return until beginning of afternoon surveys. This allowed all possible basking locations to be observed while minimizing disturbance to the turtles. The identity and location of each turtle basking at the time of the survey were recorded. Turtles that left one basking location and began basking at another during the survey were only noted at their initial location. A turtle was considered to be basking when it was stationary with its carapace completely or partially out of the water, as is consistent with a definition of atmospheric basking (Chessman 1987). During these surveys, it was not possible to record data blind because our study involved observing focal animals in the field.

All known basking structures ($n = 118$) in Wolf Howl Pond were marked with numbered pin flags in the spring of 2019 (Fig. S1). When turtles were observed basking on an unmarked structure, the structure's location was noted and marked to allow for consistent identification. A total of 77 additional structures were added after they were used by turtles over the two years of surveys. Basking structures in Wolf Howl Pond vary greatly in size and shape. Many structures are large enough to support multiple individuals or groups of basking turtles who could plausibly be unaware of each other's presence by virtue of obstructed sightlines or excessive distance between individuals. The visual capabilities of emydid turtles are largely unknown, although tortoises (Testudines: Testudinidae) and sea turtles (Testudines: Cheloniidae) have highly adept visual perception (Mäthger et al. 2007; Wilkinson et al. 2010). Red-footed Tortoises follow the gaze of a conspecific within an 80 cm-long enclosure (Wilkinson et al. 2010), suggesting a confirmed sight range of at least 80 cm in Testudines. So, we conservatively subdivided basking structures into 60 × 60 cm quadrats. Turtles sharing a structure (or quadrat, when structure division was necessary) were considered to be basking in a group. Turtles more than 60 cm apart were considered to be basking alone. We considered two turtles basking at a distance greater than 60 cm to be socially independent of each other, such that they were not exhibiting tolerance of each other. We acknowledge that our definitions of grouped and solitary basking do not account for the possible role of chemoreception in communication between individuals.

Genetic data collection & relatedness analysis

Blood samples were collected from the caudal vein of turtles during the 2018, 2019, and 2020 active seasons. Samples were drawn using sterilized BD Ultra-Fine™ 1 mL insulin syringes. Approximately 100 µL of blood was sampled from each turtle. Samples were stored on Whatman FTA®cards (Owen 2011; Whatman, Inc.). DNA extraction and single-nucleotide polymorphism (SNP) genotyping of all samples was performed by Diversity Arrays Technology, Canberra, Australia (Jaccoud et al. 2001), and yielded a dataset with 66,832 loci and mean call and reproducibility rates of 82.651 ± 0.200% and 97.854 ± 0.025% (mean ± standard error), respectively.

Filtering of genotypic data (Table S1) was performed in R version 4.0.2 (R Development Core Team 2020) using the package *'dartR'* (Gruber et al. 2018). During filtering, we removed any monomorphic loci. When multiple polymorphisms were found within the same sequence, a single polymorphism was selected at random to minimize physical linkage of loci (Lemay and Rusello 2015). We retained loci with a call rate and a reproducibility rate ≥ 99%. We calculated allelic coverage, and removed loci with read depths ≤ 2 and ≥ 7 (Lemay and Russo 2015). Loci with minor allele frequencies ≤ 2% were filtered, as high minor allele frequency can bias genotypic data (Roesti et al. 2012). When two loci had a Hamming distance (number of base differences) ≤ 25%, one locus was randomly selected to be included in the final dataset. We also filtered loci that differed significantly from Hardy-Weinberg Equilibrium ($\alpha < 0.05$). The final filtered dataset had 1015 loci, and call and reproducibility rates of 99.57 ± 0.0031% and 99.62 ± 0.0032%, respectively.

Post-filtering, we estimated pairwise relatedness between individuals in the program COANCESTRY (Wang 2011). First, we simulated multilocus data based on allelic frequencies from our genotypic dataset to select the appropriate relatedness estimator for the Wolf Howl Pond turtle population, because the accuracy of relatedness estimates depends on the genetic structure of a population (Van de Casteele et al. 2001; Wang 2011). We simulated 100 individuals with each of the following relatedness values: $r=0.000$ (unrelated), $r=0.031$ (second cousin), $r=0.125$ (first cousin), $r=0.250$ (half-sibling/avuncular/grandparent-grandchild), and $r=0.500$ (full sibling/parent-offspring). We calculated pairwise relatedness estimates for each of these simulated individuals using seven relatedness estimators (Table S2; Queller and Goodnight 1989; Li et al. 1993; Ritland 1996; Lynch and Ritland 1999; Wang 2002; Milligan 2003; Wang 2007). We then calculated Pearson correlation coefficients (*Pearson's r*) between actual relatedness of simulated individuals and estimated relatedness by each of the seven estimators. Triadic maximum likelihood relatedness estimates were most closely correlated to the true relatedness of the simulated individuals (Pearson's $r=0.996$; Table S2), and thus were used to estimate relatedness of turtles in our study population (Fig. S2).

Social network analyses

We carried out several steps to for these analyses. The first step involved constructing four types of networks that contained: (1) all individuals and all their associations, (2) all individuals and their preferred associations, and two sex-specific networks (3 and 4) that included all of their respective associations (see details in the "Social network construction" section). We also quantified the spatial overlap of all individuals studied, so that we could control for it in downstream analyses (see details in "*Quantifying spatial overlap*" section). We analysed the social association data at two complementary levels: dyadic and individual. To analyse factors impacting turtle social associations at the dyadic level, we used the multiple regression quadratic assignment procedure with double semi-partialing ($\mathrm{MRQAP_{dsp}}$) (see details in "*Drivers of social associations*" section). At the individual level, we analysed social behaviour using linear models (see details in "*Drivers of social structure*" section).

Social network construction

Before network construction, we examined whether data from our two study years could be combined using a multiple regression quadratic assignment procedure with double semi-partialing ($\mathrm{MRQAP_{dsp}}$) using the function *'mrqap.dsp'* in the R package *'asnipe'* (Krackhardt 1988; Dekker et al. 2007; Farine 2013). $\mathrm{MRQAP_{dsp}}$ is a permutation test for calculating multiple linear regression coefficients for data matrices, and can be interpreted similarly to a multiple regression, such that one variable can control for the effect of another. This method is commonly used in social network analyses, where parallel matrices of pairwise data for a set of focal individuals are correlated (Dekker et al. 2007). We found that associations between individuals were significantly and positively correlated across study years ($\beta=0.070$, $p=0.042$, Pearson's $r=0.005$). Accordingly, all social networks were constructed using pooled data from both years of basking surveys.

We constructed four networks of social associations among basking Midland Painted Turtles in Wolf Howl Pond (Farine and Whitehead 2015): three that examined overall associations and one that examined preferred associations. The first network contained all turtles observed eight or more times during basking surveys ($n=88$). This network was constructed because spatial overlap estimations (as described below) were not accurate for turtles observed less than eight times. The second and third networks contained all observed individuals of each sex ($n=157$ females in one network; $n=32$ males in another network). These sex-specific networks were used for calculating four social network metrics (binary degree, weighted degree, coefficient of variation of edge weights, and betweenness) and for examining relationships between these metrics and two predictor variables with linear models (see below "*Drivers of social structure*"). Female turtles in Wolf Howl Pond are significantly larger than males ($t=-6.42$, df$=46.64$, $p<0.001$), so the sexes were analyzed separately to allow for the inclusion of body size as a predictor variable in our analyses. Juveniles, defined as turtles with a midline carapace length (midCL)<9 cm or for whom sex could not be accurately determined, were not included in any social networks. Under our fieldwork protocols, we are unable to give turtles with a midCL under 9 cm any identifying carapace markings; therefore, we were unable to determine the identity of any juvenile turtle observed basking.

Within each network, association strength for each possible dyad (pair of turtles) was calculated using the Half-Weight Index (HWI), which ranges from 0 (dyad never in the same group during any basking survey) to 1 (dyad together during all basking surveys). HWI is commonly used to analyze grouping data where the complete population is unlikely to be observed in a sampling period (Cairns and Schwager 1987; Whitehead 2008), as is the case with our study population. Networks were weighted and undirected, such that nodes were connected when HWI>0 between them. Networks were constructed using the R package *'asnipe'* with the functions *'get_group_by_individual'* and *'get_network'* (Farine 2013).

The fourth network contained calculated preferred social associations between turtles. Across animal taxa, individuals have been documented to preferentially invest time with certain group members with whom they associate more often than by chance alone (Croft et al. 2004; Riley et al. 2021; Gomes et al. 2022). The biological drivers (i.e., demographics, morphology, personality) of preferred associations can differ from that of all the interactions in which an individual engages (Whitehead et al. 1999). Thus, we opted to investigate both all and preferred associations of Midland Painted Turtles in our study to understand whether individual choice plays a role in this species' social structure, and to obtain a fuller picture of the factors that drive different types of social interactions. To calculate preferred associations, we determined the mean HWI value (0.0216) across all possible pairings and designated all associations greater than twice this mean value as preferred (Gero et al. 2015; Riley et al. 2021). All associations with a HWI less than twice the mean (HWI $<$ 0.0431) were given a value of 0 in the resultant network of preferred associations (i.e., they were not preferentially associated). All other HWI values of (preferred) associations were left as calculated, so that they reflected the strength of the association (i.e., varied between 0.0435 and 0.4314). The networks for all turtles in our population that contained HWI for overall and preferred social associations were used to test relationships between social associations and four predictor variables (genetic relatedness, spatial overlap, sex, and body size) using two separate MRQAP$_{dsp}$ analyses (see below "*Drivers of social associations*").

Quantifying spatial overlap We quantified space use by turtles based on location observations of basking in nine discrete clusters of basking habitats across Wolf Howl Pond (Fig. S1). This approach was used because the turtles appeared to exhibit low site-specific fidelity, but high fidelity to a general area with a number of suitable basking structures (J. Kentel and CJR, pers. obs.). Calculations of spatial overlap were not accurate for turtles observed less than eight times during basking surveys; therefore, we examined spatial overlap only for individuals observed eight or more times (n = 88) using a Bray-Curtis dissimilarity matrix (*BC*; Bray and Curtis 1957), such that:

$$BC_{xy} = 1 - \frac{2C_{xy}}{S_x + S_y}$$

where C is the number of clusters in which both individuals x and y were observed, and S is the total number of clusters in which each individual was observed. Lower *BC* values between pairs of individuals in a dyad reflect more overlap in space use, whereas higher *BC* values indicate less overlap in space use. We included this *BC*-dissimilarity matrix of spatial overlap in analyses examining the predictors of turtle social associations to investigate the role space-use may play in turtle social interactions (see below "Drivers of social associations").

Testing framework for drivers of social associations and structure Hypothesis testing frameworks for social network data have well-documented challenges due to non-independence (Puga-Gonzalez et al. 2019; Farine and Carter 2021; Hart et al. 2022). Single permutation approaches have been used to address this challenge, but they can suffer from high rates of type I and II errors (between 35 and 60% depending on method; Puga-Gonzalez et al. 2019). In recent years, methods to alleviate elevated error rates have been proposed, including well-specified parametric models (Hart et al. 2022), restricted node permutations, testing multiple hypotheses, and a double permutation approach (Farine and Carter 2021). We opted to use the double permutation approach because, through simulations, it was found to do a better job of reducing error rates than single permutation approaches. Below (in sections, "*Drivers of social associations*" and "*Drivers of social structure*") we describe how the double permutation approach was applied in our analyses.

Drivers of social associations Two separate MRQAP$_{dsp}$ analyses were performed to test for relationships between overall and preferred associations (HWI), respectively, and four predictor variables: genetic relatedness, spatial overlap, sex, and body size (midCL; Krackhardt 1988; Dekker et al. 2007; Farine 2013). The sex difference matrix was constructed using a binary code, such that dyads consisting of individuals of the same sex were coded as "1" and dyads of different sexes were coded as "0". The body size matrix was constructed using the absolute value of the difference in midCL between the two individuals in each dyad. We used a double permutation approach, which involved performing 10,000 pre-network permutations to determine the deviation of HWI in the dataset prior to running the MRQAP$_{dsp}$. We then compared observed HWI to randomly expected HWI for all edges in the network (associations between turtles) and calculated residuals. These HWI residuals were then the response variable that was fit into the MRQAP$_{dsp}$ to test for relationships between HWI and predictors (Farine and Carter 2021). All MRQAP$_{dsp}$ were run with 10,000 permutations. MRQAP$_{dsp}$ does not calculate R^2_{adjusted} for each predictor in the model, rather an R^2_{adjusted} for the entire model is calculated. We therefore reported *Pearson*'s *r* values calculated using the R function *'mantel'* from the R package *'vegan'* (R Development Core Team 2020). However, these values do not take into account other predictor variables in the model; instead, they estimate a correlation strictly between the response variable and a single predictor variable.

Drivers of social structure Linear models in the base R function *'lm'* (R Development Core Team 2020) were used to determine how individual attributes (i.e., body size, midCL, and a proxy of boldness) affected individual social behaviour in Painted Turtles. We calculated four network metrics – binary degree, weighted degree, coefficient of variation of edge weights (CV), and betweenness – separately for males and females based on their social association (HWI) networks (Table 1). We also used a double-permutation approach for analyses of these network metrics (Farine and Carter 2021). This involved performing 10,000 permutations of a random network of social association between individuals, and then calculating values for each metric for all randomly-created individuals. We calculated residuals by subtracting the median random value from the observed value of each metric for each individual. These residual values for each sex's four network metrics were the response variables fit into separate linear models (Farine and Carter 2021). These separate linear models each included body size, a proxy of boldness, and their interaction as predictor variables. If the interaction was not significant, models were re-run without it to allow interpretation of main effects. Our proxy of boldness was estimated using capture frequency, which was specifically calculated for each individual as the total number of captures divided by the number of years they were part of this long-term study (possible maximum of 30 years). Mark-recapture of turtles at Wolf Howl Pond has remained consistent in timing (May-June annually), effort (2–5 researchers), and capture method (dip-netting from canoe) over the 30 years of study, so any logistical impacts on capture frequency were minimized. Capture frequency ranged from 0.38 to 1.0, and this variability likely represents the fact that some turtles are more or less "trap-" or "catch-happy" (Frazer et al. 1990; Deforce et al. 2004; Koper and Brooks 1998; Sunnucks 1998; Garamszegi et al. 2009; Tyrrell et al. 2009; Reinhardt and Hrodey 2019; Hollender et al. 2022). While our proxy of boldness is not a direct quantification of behaviour with a standard assay (e.g., a simulated predator attack; Pich et al. 2019; Blanchett et al. 2024; Carlson et al. 2024; Gan et al. 2024), our rationale is that turtles caught more often may also be more inclined to take greater risks, as indicated by spending more time higher in the water column, and atmospherically basking in close proximity to researchers. Thus, we used this proxy because bolder animals are more likely to be captured by trap or hand (Garamszegi et al. 2009; Carter et al. 2012; Ward-Fear et al. 2019; but see Michelangeli et al. 2016; Johnstone et al. 2021) and because other studies have used catchability as a measure of boldness (Wilson et al. 1993; Réale et al. 2007; Wilson et al. 2011; Carter et al. 2012).

Table 1 Network metrics of individual social behaviour measured in the Wolf Howl Pond (Algonquin Provincial Park, Ontario, Canada) population of Midland Painted Turtles (*Chrysemys picta marginata*). Metrics were calculated based on definitions from Whitehead (2008) manually or using the R packages *'raster'* and *'sna'* (Csardi and Nepusz 2006; Butts 2019; R Development Core Team 2020)

Metric	Formula	Definition	Source
Binary degree	$bd_x = n_{edges}(x)$	Number of edges connected to a focal node. Individuals with a higher binary degree have known associations with a higher number of individuals.	Coded manually (based on the definition from Whitehead 2008).
Weighted degree	$s_x = \sum_x \alpha_{xy}$	Sum of HWI of all edges connected to a focal node. Individuals with a higher weighted degree have a combination of stronger and more numerous associations with other individuals.	Coded manually (based on the definition from Whitehead 2008).
Coefficient of variation of edge weights (CV)	$c_{xy} = \frac{\sum_x \sum_z \alpha_{xy}\alpha_{xz}\alpha_{yz}}{\max \alpha_{yz} \sum_y \sum_z \alpha_{xy}\alpha_{yz}}$	Heterogeneity of edges connected to a focal node. Individuals with a higher CV demonstrate more variability in their social associations.	*raster::cv*
Betweenness	$B_x = \sum_{y,z:y\neq z,y\neq x,z\neq x} \frac{g_{xyz}}{g_{yz}}$	The number of most parsimonious paths between non-directly connected nodes that pass through a focal node. Individuals with a higher betweenness act as a 'bridge' between dyads within a social network; thus, they are the connection to more individuals.	*sna::betweenness*

x, *y*, and *z* are individuals (nodes) in a social association network. α_{xy} is the half weight association index (HWI) value between individuals *x* and *y*. *g* is the index of the graph for which betweenness is being calculated.

During data exploration prior to running models (Zuur et al. 2010), midCL and boldness did not substantially co-vary (R^2_{adjusted}=0.02; Fig. S3), suggesting that larger turtles were not bolder than smaller turtles. We also examined each network metric to ensure normality, lack of outliers, and lack of collinearity. Assumptions of residual normality and homogeneity of variance were ensured before model interpretation for all linear models (Zuur et al. 2010). Significance testing of data generated from social networks is based on comparison of observed data to random permutations of a null model (Farine and Whitehead 2015; Farine and Carter 2021). *P* values (p_{rand}) were calculated by comparing observed model coefficients (based on data corrected by double permutation; Farine and Carter 2021) for each predictor variable to the range of coefficients for all random permutations of its corresponding model (Farine and Whitehead 2015; Leu et al. 2016). Effects were considered significant if the observed coefficients were outside the 95% range of the random model coefficient distributions (Farine and Whitehead 2015).

Results

Social organization in basking aggregations

We observed 3898 instances of turtles basking; of these observations, 2869 were of females, 536 were of males, and, although they were both excluded from analyses below, we also observed juveniles 18 times and individuals of unknown sex 475 times. We observed 937 total communal basking events, and 817 instances of solitary basking (Fig. 1). Basking aggregations ranged in size from 2 to 24 individuals, with a mean size of 2.22 ± 2.02 (standard deviation) and a median of 2 individuals. Specifically, 51% (482/937) of groups were of 2 turtles, 21% (199/937) were of 3 turtles, 11% (100/937) were of 4 turtles, 6% (57/937) were of 5 turtles, and the remaining group sizes (6–13, 17–20, 23, 24) did not individually make up more than 4% of observations. The majority of groups were made up of individuals of the same sex but, within mixed-sex aggregations (18% of all groups), the sex ratio was variable and ranged from nine females per male to three males per female. The composition of aggregations containing more than two individuals was never repeated during our study, but pairs of individuals were observed in the same aggregation multiple times. Specifically, unique pairs were observed aggregating across a maximum of 36% of surveys. This repeatability of the same pair of individuals in the same group was exemplified by a pair that was observed together in 52 out of a possible 79 surveys (66% of observations).

Social associations and their drivers

Summary of association strength Mean HWI between the 88 turtles included in our analyses was 0.022 ± 0.038 (mean ± standard deviation). All HWI ranged from 0.00 to 0.43. In a comparison of this observed level of social association against what one may expect by chance (i.e., 10,000

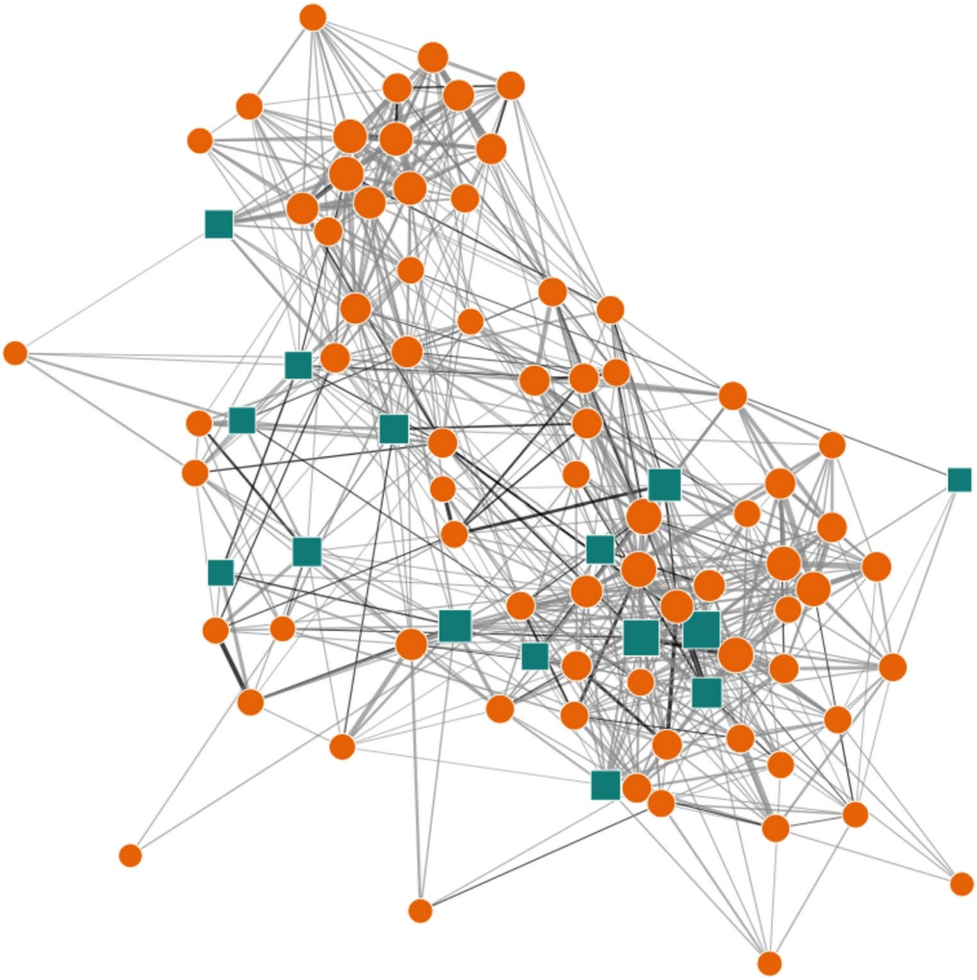

Fig. 1 Social network diagram of preferential social associations among Midland Painted Turtles (*Chrysemys picta marginata*; $n = 88$) in Wolf Howl Pond (Algonquin Provincial Park, Ontario, Canada). Females are denoted by orange circles ($n = 73$), and males by turquoise squares ($n = 15$). Nodes (circles and squares) are sized relative to the individual's number of associations. Edge width (lines connecting circles and squares) is based on the strength of association between the terminal nodes. Edges are colored based on estimated relatedness between associating turtles, such that $r > 0.125$ between two individuals (a first cousin relationship or greater) results in a black edge, and $r < 0.125$ results in a grey edge

Table 2 Output of the multiple regression quadratic assignment procedure with double semi-partialing ($\mathrm{MRQAP_{dsp}}$) analyzing overall half weight association indices (HWI) and attribute matrices (genetic relatedness, difference in midline carapace length, spatial overlap, and sex similarity) for Midland Painted Turtles (*Chrysemys picta marginata*; $n=88$) from Wolf Howl Pond (Algonquin Provincial Park, Ontario, Canada). $\mathrm{MRQAP_{dsp}}$ was run with 10,000 permutations. *Pearson*'s r values between the HWI and respective predictor variables were calculated using the R function *'mantel'* from the R package *'vegan'*. Superscript (*) denotes a significant effect or correlation ($\alpha<0.050$)

	β	p		Pearson's r
Intercept	0.008	0.012	*	-
Genetic Relatedness	−0.016	0.279		−0.018
Body Size Difference	<0.001	0.723		0.003
Spatial Overlap	−0.005	0.182		−0.032
Sex Similarity	<0.001	0.960		0.006

Model $R^2_{\text{adjusted}} = < 0.001$

Table 3 Output of the multiple regression quadratic assignment procedure with double semi-partialing ($\mathrm{MRQAP_{dsp}}$) of preferred half weight association indices (HWI) and attribute matrices (genetic relatedness, difference in midline carapace length, spatial overlap, and sex similarity) for Midland Painted Turtles (*Chrysemys picta marginata*; $n=88$) from Wolf Howl Pond (Algonquin Provincial Park, Ontario, Canada). $\mathrm{MRQAP_{dsp}}$ was run with 10,000 permutations. *Pearson*'s r values between the HWI and respective predictor variables were calculated using the R function *'mantel'* from the R package *'vegan'*

	β	p	Pearson's r
Intercept	0.001	0.730	-
Genetic Relatedness	−0.005	0.713	−0.006
Body Size Difference	<0.001	0.922	−0.006
Spatial Overlap	−0.006	0.146	−0.035
Sex Similarity	<0.001	0.922	0.005

Model $R^2_{\text{adjusted}} = < 0.001$

randomly permuted networks; see Supplementary Materials for details), we found that Painted Turtles at Wolf Howl Pond associate more than expected ($p=0.005$, Fig. S4). Out of all dyads, 39% (1509/3916) had a HWI > 0 and of those, 42% (675/1590) were preferential (e.g., with a HWI > 0.0431; see details above).

Genetic relatedness Mean pairwise genetic relatedness between the 88 turtles included in our analyses was 0.013 ± 0.045 (mean ± standard deviation). Relatedness (r) estimates ranged from 0.000 to 0.500. We detected 22 parent-offspring/full sibling dyads ($r=0.500$), 26 half-sibling/avuncular/grandparent-grandchild dyads ($r=0.250$), 136 first cousin dyads ($r=0.125$), and 3732 unrelated dyads ($r=0.000$). Genetic relatedness was not a significant predictor of overall HWI ($p=0.28$; Table 2) or preferred HWI ($p=0.71$; Table 3). Preferred associations tended to be more common between unrelated and first cousin dyads. Specifically, preferred associations were documented in 17% (643/3732) of unrelated dyads, 20% (27/136) of first cousin dyads, 11% (3/26) half-sibling/avuncular/grandparent-grandchild dyads, and 9% (2/22) parent-offspring/full sibling dyads.

Size difference The average size difference (midCL) between the 88 turtles included in our analyses was 1.67 ± 1.26 cm (mean ± standard deviation). Differences ranged from 0.00 cm to 6.94 cm. Size difference was not a significant predictor of overall HWI ($p=0.72$; Table 2) or preferential HWI ($p=0.92$; Table 3).

Spatial overlap Mean space use dissimilarity (BC) between the 88 turtles included in our analyses was 0.39 ± 0.27 (mean ± standard deviation) and ranged from 0.00 to 0.98. Spatial overlap was not significantly related to overall HWI ($p=0.18$; Table 2) or preferential HWI ($p=0.15$; Table 3).

Sex similarity The sample of 88 turtles included in our analyses contained 73 females and 15 males. Sex similarity was not a significant predictor of overall HWI (p = 0.96; Table 2) or preferred HWI (p = 0.92; Table 3).

Factors affecting individual social behaviour

Binary degree was significantly affected by body size ($p_{\text{rand}} < 0.001$), boldness ($p_{\text{rand}} < 0.001$), and their interaction ($p_{\text{rand}} < 0.001$) in females, such that the number of females with which a focal turtle associated was higher for larger turtles and the strength of this positive relationship lessened with increasing boldness (Fig. 2; Table 4). In males, binary degree was not associated with body size or boldness (Table 5).

Weighted degree was significantly affected by body size ($p_{\text{rand}} < 0.001$), boldness ($p_{\text{rand}} < 0.001$), and their interaction ($p_{\text{rand}} < 0.001$) in females, such that weighted degree (representing the strength of that individual's associations) decreased with increasing body size but the strength of this negative relationship lessened with increasing boldness (Fig. 2; Table 4). In males, weighted degree was not associated with body size or boldness (Table 5).

CV was significantly affected by body size ($p_{\text{rand}} < 0.001$), boldness ($p_{\text{rand}} < 0.001$), and their interaction ($p_{\text{rand}} < 0.001$) in females, such that variability in social interactions decreased with increasing body size but the strength of this negative relationship was lessened with increasing boldness (Fig. 2; Table 4). In males, CV was not associated with body size or boldness (Table 5).

Betweenness was significantly affected by body size ($p_{\text{rand}} < 0.001$) in female turtles such that smaller turtles were more connected to conspecifics (i.e., were associated more with turtles who were also associated with each other; Table 4). There was no significant relationship between betweenness and boldness in females ($p_{\text{rand}} = 0.76$). In males, betweenness was not significantly affected by body size or boldness (Table 5).

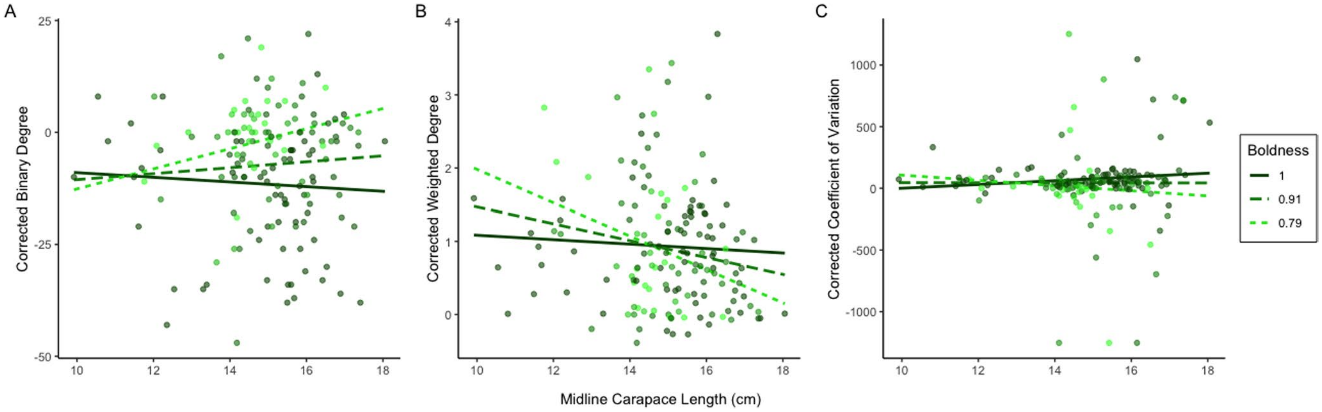

Fig. 2 Relationship between three descriptive metrics of social behaviour (A, binary degree; B, weighted degree; and C, coefficient of variation) and the interaction between body size (midline carapace length) and boldness observed in female Painted Turtles ($n = 157$). Three lines of best fit represent the relationship at different levels of turtle boldness: a capture frequency of 79% (mean – 1 SD), 91% (mean), and 100% (max). These lines of best fit were generated using the R package *‘interactions’* (Long 2024). Points represent individual turtles and are coloured according to the individual’s boldness (capture frequency). Model predictions were made based on 1,000 permutations

Discussion

Our study explores potential drivers of social associations and behaviour of Midland Painted Turtles during basking in the wild. When considering all the turtles observed in our study, the majority (79%) of individuals were within aggregations; yet, when considering observations of basking events, only 53% of basking events included two or more turtles. The social organization (i.e., group size and composition; Kappeler 2019) exhibited by basking turtles was most commonly pairs of turtles that were the same sex. None of the factors we tested as possible drivers of the observed social associations (quantified using the half weight index, HWI) were significant; these included spatial overlap, genetic relatedness, and sex and body size similarity. Although these factors influence population-level social associations in other basking reptiles (Gardner et al. 2016; Bull et al. 2017; Whiting and While 2017; Riley et al. 2021), they do not appear to influence basking associations of wild Painted Turtles that we studied. When considering social associations amongst turtles at Wolf Howl Pond, they were stronger than we would expect from chance alone, but only about one third of dyads had a HWI greater than zero (indicative of a social association). Interestingly, out of the social associations that did occur between turtles (dyads with HWI > 0), close to half (42%) were preferred. This suggests that when turtles did associate with one another, they were within preferred associations. Lastly, we examined turtle social behaviour using four network metrics separately for each sex. We found a significant impact of body size in females and this effect was counteracted by a female’s boldness in three out of four metrics (weighted and binary degrees, and CV; Table 1). These metrics quantified the number and strength of associations maintained by a turtle, the variability of social associations, and how connected an individual was within the social network. In contrast to our findings for females, the social behaviour of males was not impacted by body size or boldness. These findings suggest that a social hierarchy (based on body size and behaviour) may influence basking at the individual-level for females, but not males. Together, our results suggest that social interactions occur within basking aggregations of emydine turtles, but the function of and differences between random and preferential associations needs further exploration. In addition, examination of the drivers of basking aggregations across different populations of Painted Turtles and other turtle species will be critical for understanding variability of social behaviour within Chelonians.

We found that common factors that influence social associations of animals (i.e., spatial proximity, kinship, sex and size similarity) did not impact basking aggregations of Painted Turtles. These findings suggest that basking associations are not sex- or size-assortative. It is particularly notable that spatial overlap and relatedness did not impact associations, as these factors are known to impact other reptile groups (Chapple 2003; Gardner et al. 2016). In particular, spatial overlap due to sharing of potentially limited resources is often cited as a starting point for the evolution of more complex forms of sociality (Graves and Duvall 1995; Hatchwell and Komdeur 2000). Basking habitat in Wolf Howl Pond is not limited, as no more than 40 of a possible 195 basking locations were simultaneously used by turtles during a basking survey, so resource limitation does not seem to be driving aggregations in our study population. Thus, a lack of an impact of spatial overlap on Painted Turtle basking aggregations, even though fidelity for

Table 4 Summary statistics of significance testing of social network metric data for **female** Midland Painted Turtles (*Chrysemys picta marginata*; $n=157$) in Wolf Howl Pond (Algonquin Provincial Park, Ontario, Canada). The effects of body size (midCL), boldness, and the interaction between these two variables were examined. We generated 10,000 permutations for each random network. Coefficient ranges that are presented for random network permutations span 95% of randomized coefficients. Effects are considered significant if the observed coefficient is outside the 95% range of randomized coefficients ($\alpha=0.05$). When the interaction variable was non-significant, it was removed from reported models and they were re-run. This is denoted using "---". Significant effects are denoted by superscript asterisks (*)

Metric	Model Variables	Observed β	Random β Range	p_{rand}
Binary degree	Intercept	−147.44	8.60 to 207.59	<0.001*
	Body Size	12.22	−9.71 to 3.19	<0.001*
	Boldness	139.22	−98.59 to 97.29	<0.001*
	Body Size x Boldness	−12.42	−8.35 to 4.56	<0.001*
Weighted degree	Intercept	12.07	−2.27 to 6.93	<0.001*
	Body Size	−0.77	−0.29 to 0.32	<0.001*
	Boldness	−10.53	−2.93 to 6.03	<0.001*
	Body Size x Boldness	0.73	−0.51 to 0.11	<0.001*
Coefficient of variation of edge weights	Intercept	1428.25	−2505.13 to 765.06	<0.001*
	Body Size	−104.96	−56.94 to 191.13	<0.001*
	Boldness	−1450.73	−1194.77 to 2432.70	<0.001*
	Body Size x Boldness	110.07	−166.56 to 105.05	<0.001*
Betweenness	Intercept	251.77	491.80 to 925.74	<0.001*
	Body Size	−10.96	−44.10 to −17.89	<0.001*
	Boldness	−72.55	−138.00 to 130.40	0.764
	Body Size x Boldness	---	---	---

Table 5 Summary statistics of significance testing of social network metric data for **male** Midland Painted Turtles (*Chrysemys picta marginata*; $n=32$) in Wolf Howl Pond (Algonquin Provincial Park, Ontario, Canada). The effects of body size (midCL), boldness, and the interaction between these two variables were examined. We generated 10,000 permutations for each random network. Coefficient ranges that are presented for random network permutations span 95% of randomized coefficients. Effects are considered significant if the observed coefficient is outside the 95% range of randomized coefficients ($\alpha=0.05$). When the interaction variable was non-significant, it was removed from reported models and they were re-run. This is denoted using "---"

Metric	Model Variables	Observed β	Random β Range	p_{rand}
Binary degree	Intercept	15.08	−41.39 to 77.69	0.567
	Body Size	−0.31	−2.42 to 1.33	0.639
	Boldness	−13.33	−69.78 to 46.29	0.160
	Body Size x Boldness	---	---	---
Weighted degree	Intercept	1.94	−3.23 to 5.99	0.132
	Body Size	−0.06	−0.17 to 0.11	0.133
	Boldness	−0.87	−3.76 to 2.98	0.132
	Body Size x Boldness	---	---	---
Coefficient of variation of edge weights	Intercept	46.64	−1333.85 to 1404.31	0.411
	Body Size	0.46	−39.15 to 65.39	0.758
	Boldness	−9.16	−1204.91 to 931.18	0.429
	Body Size x Boldness	---	---	---
Betweenness	Intercept	74.71	−224.77 to 306.78	0.151
	Body Size	−1.10	−7.73 to 8.74	0.286
	Boldness	−59.94	−278.73 to 154.73	0.119
	Body Size x Boldness	---	---	---

certain basking areas was observed at our site, potentially reflects the lack of strong social associations we observed in the majority (2/3) of dyads. Kinship is also known to be a driver of social association in other reptile species, and across the animal kingdom (reptiles: Bull et al. 2001; Clark 2004; O'Connor and Shine 2004; Galoyan 2013; Riley et al. 2021; mammals: Paolucci et al. 2006; Wittemyer and Getz, 2007; birds: Painter et al. 2003), including hatchlings of one turtle species when raised in captivity (Diamondback Terrapin, *Malaclemys terrapin*; Rife 2007). Our capacity to assess the influence of relatedness on Painted Turtle social behaviour was limited by the low levels of close kinship (i.e., $r>0.125$) detected in our study population; other turtle populations with higher numbers of close kin should be investigated. Although there was no evidence for kin-biased social associations in Painted Turtles, individual fitness benefits still could potentially be gained from basking in a group. For example, the 'many-eyes' hypothesis explains how animals in groups, regardless of relatedness, receive antipredator benefits from shared vigilance (Fairbanks and Dobson 2010; Olson et al. 2015), and larger basking groups of Painted Turtles flee sooner than smaller groups (Fenech 2023). Further, female Painted Turtles in our study population cue on conspecific presence for nest site selection (Kell et al. 2021), and communal basking may be making use of social information in a similar way. Another potential limitation of our study is that the population is female-biased, with approximately three females per male (Moldowan et al. 2020). Accordingly, the majority of basking observations were of females and female-dominated basking aggregations. The smaller sample size of male turtles could have impacted our ability to find significant effects; however, our total observations of male turtles ($n = 621$) was likely sufficient to detect significance, even in a network with low correlation (Hart et al. 2021).

The fitness benefits and costs of social interactions vary greatly in animal populations. In most animals, social associations result from both random encounters of individuals in space and time, as well as individuals actively seeking interactions with certain conspecifics (Spiegel et al. 2016). Variation between individuals in the benefits received from social association is particularly extreme in populations with stable, linear social hierarchies, as subordinates often suffer fitness consequences from dominant individuals through attacks, lack of access to food, or exclusion from high-quality areas with low predation risk (Riley et al. 2017; Evans and Morand-Ferron 2019). In this case, individuals may prioritize associations with individuals with whom they have previously had positive experiences (i.e., the 'social preference' hypothesis; Evans and Morand-Ferron 2019). We found that the majority of Painted Turtles did not associate with one another, but for those that did, 42% were preferred associations. Other reptiles also have preferential social associations with conspecifics (Arizona Black Rattlesnakes, *Crotalus cerberus*: Schuett et al. 2017; Eastern Water Dragons, *Intellagama lesueurii*: Strickland et al.2014, Piza-Roca et al. 2019; Eastern Gartersnakes, *Thamnophis sirtalis sirtalis*; Skinner and Miller 2020; Tree Skinks, *Egernia striolata*: Riley et al. 2021). In some cases, the preferential associations are kin-biased (*Intellagama lesueurii*: Piza-Roca et al. 2019; *Egernia striolata*: Riley et al. 2021). In contrast, we found that Painted Turtle preferred social associations, during basking, were not biased towards kin. More research is needed to understand the factors that are guiding preferential associations between Painted Turtles. For example, perhaps similar space- or resource-use in Wolf Howl Pond may guide repeated associations of individuals, yet we did not find evidence that spatial overlap related to association in this study. Also, the 'social preference' hypothesis may afford insights into where to direct future research (Evans and Morand-Ferron 2019). Based on this hypothesis, our finding of high variability in social associations, including a small, subset of preferential associations, may suggest there is a stable, social hierarchy present in basking aggregations within Wolf Howl Pond. Familiarity and the quality of previous social interactions (i.e., tolerance instead of aggression) are known to influence strength and stability of social associations across diverse taxa (Dugatkin and Alfieri 1991; Carter et al. 2020; Fox et al. 2024), and thus should be a future starting point for studies examining the factors that explain preferred associations during basking in turtles.

Social behaviour of animals, including turtles, can be influenced by morphology and behaviour (Moldowan et al. 2020; Koprowski et al. 2024). Indeed, we found that social behaviour of female turtles during basking was influenced by body size and boldness. Body size determines competition success in turtles (Auth 1975; Pluto and Bellis 1986; Lindeman 1999), and is a critical determinant of their mating preferences and tactics (Liu et al. 2013; Moldowan et al. 2020). In our study population, larger female turtles had more social associations (binary degree) that were weaker (weighted degree), less variable (CV), and less interconnected (betweenness) than those of smaller individuals. These findings suggest that larger females, who could be socially dominant, may preferentially bask in high-quality habitat more consistently and for longer, leading to more social associations because many turtles may visit these preferred basking sites. Yet, individuals that visit these sites may not, in turn, associate with one another. In contrast, if they are dominant individuals, they may be aggressive towards visitors (Koprowski et al. 2024) and, thus, in general have fewer, preferential relationships with other individuals. Interestingly, the effect of body size on female turtle social behaviour was mediated by our proxy of boldness, suggesting that these two factors together influence turtle social interactions. For small turtles, bolder individuals had more associations than shyer turtles. In contrast, for large turtles, bolder individuals had fewer associations than shyer turtles. This was also true for the strength and variability of their associations: bold, small turtles had weaker and less variable associations than shyer, small turtles. Large, bold turtles had stronger and more variable associations than large, shy turtles. In terms of basking associations, boldness may result in a less-sensitive flight response (Cooper 2009, 2012). Accordingly, boldness may affect an individual turtle's likelihood of terminating basking due to a perceived risk, which would also impact their social interactions during basking. Overall, there appear to be multiple factors influencing social behaviour of female Painted Turtles at the individual level.

Our study on the social aspects of basking behaviour in Painted Turtles highlights opportunities for continuing research on turtle sociality. Our study suggests there is nuance to Painted Turtle social interactions during basking, especially in females, which supports previous research that found that during nesting, females may cue on conspecific behaviour for nest site selection (Kell al. 2021). Future researchers could conduct surveys over a larger per-survey timeframe, and focus on particular areas of basking habitat to observe interactions between individuals (i.e., expression of aggressive vs. tolerance behaviours; Bury and Wolfheim 1973; Koprowski et al. 2024). While our survey style was comprehensive in that it covered the entirety of available basking habitat within Wolf Howl Pond, its static nature prevented the observation of any interaction between individuals beyond their grouped presence or lack thereof. Evidence is mounting that turtles vocalize as a form of communication (e.g., Charrier et al. 2022; Lacroix et al. 2022; Zhou et al.

2023) and, though these vocalizations have yet to be studied or otherwise documented in Midland Painted Turtles, their potential as a means of social communication should not be discounted. Further, researchers could conduct behavioural trials to directly quantify boldness using established assay framework (e.g., simulated predator attack; Pich et al. 2019; Blanchett et al. 2024; Carlson et al. 2024; Gan et al. 2024) and test, through manipulative experiments, how behavioural traits influence patterns of hierarchical social structure for which we found evidence in females. Trials could be run to examine social interactions between pairs of varying body sizes, levels of boldness, and sexes. Lastly, future work could also attempt to examine the benefits of communal basking in Painted Turtles. Researchers could examine the vigilance of grouped versus solitary baskers, especially as it has recently been found that Painted Turtles initiate escape at a further distance when in larger basking aggregations (Fenech 2023). Another line of inquiry could examine whether turtles utilise social information to cue on quality of basking locations using a framework similar to Kell et al. (2021).

Conclusion

Our observations of basking behaviour of Painted Turtles revealed novel findings about individual social interactions and behaviour of an aquatic reptile with no parental care. Our study revealed variation in an individual Painted Turtle's social associations, and that for the minority that associated, they had preferred associates. Further, body size and boldness affected the social behaviour of female turtles during basking. These findings, as well as previous research showing size-dependent mating strategies of males in our study population (Moldowan et al. 2020), suggest that a hierarchy may guide sociality of Painted Turtles in Wolf Howl Pond. Overall, our study provides first insights into social behaviour of an understudied taxonomic group, freshwater turtles, and provides a framework for further study and increases knowledge about the factors that may play a role in the evolution of vertebrate sociality more generally.

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Authors' contributions Conceived and designed the experiment: CJR, JDL, JLR. Data curation: CJR. Formal analysis: CJR, JLR. Writing – original draft: CJR, JLR; Writing – review & editing: CJR, JDL, NR, JLR. Supervision: JDL, JLR; Project administration: JDL.

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Data availability Data and code are available from an Open Science Framework repository that can be found at https://osf.io/rz95k/overview.

Declarations

Ethics approval All applicable institutional and national guidelines for the use of animals were followed. Specifically, all work involving animals was carried out under approved Laurentian University and University of Toronto animal use protocols (AUPs 2017-02-01, 20011948) that follow the Canadian Council for Animal Care standards. Also, our work was authorized by permits from Ontario Parks and the Ministry of Natural Resources.

Competing interests The authors declare that they have no conflicts of interest.

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