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Differences in activity between reproductive and non-reproductive freshwater turtles during the nesting season

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Abstract. Freshwater turtles may actively modify their behaviour, including during the reproductive season and depending on their sex or reproductive status. However, limited research has elucidated behavioural dynamics in freshwater turtles, largely because they are mostly cryptic and difficult to track in the wild. We used accelerometers to track fine-scale activity in free-ranging Blanding's and Painted turtles in southern Ontario, Canada, and assessed behavioural differences between males, gravid females, and non-gravid females during the June nesting season. We found that gravid females of both species spent more time sitting and walking, and less time underwater, compared to non-gravid females and males. We did not detect activity differences between males and non-gravid females, and responses were largely consistent between species. The difference in movement of gravid females suggests that observed variation in activity is largely driven by reproduction, for instance, prolonged periods of walking in search of nest sites. These differences in activity may lead to differential risk between sexes and help explain the prevalence of higher adult female mortality in many freshwater turtle populations. We conclude that understanding movement dynamics is crucial for expanding our understanding of the drivers of freshwater turtle ecology, as well as help support conservation planning efforts designed to benefit these at-risk species.

Keywords. freshwater turtles, bio-logging, behaviour, free-ranging animals

Introduction

Dynamic behavioural repertoires are a core component of animal ecology and conservation, with variation in activity or movement being necessary to elicit favourable individual responses to environmental heterogeneity (Mery and Burns, 2010; Boyd et al., 2016). For example, individuals may vary their activity or movement patterns in response to local or seasonal availability of resources like food or mates, or to avoid stressors like predation risk or temperature extremes (Danchin et al., 2008; Stillman, 2019; Shaw, 2020). Such responses can improve individual survival and reproduction and therefore play a defining role in fitness. Thus, understanding behavioural dynamics can not only improve our ecological insight, but also contribute to the development of robust conservation and management strategies (Berger-Tal et al., 2016; Merrick and Koprowski, 2017). Despite recent advances in technology and study design, tracking behaviour in free-ranging animals remains a substantial challenge in large part due to their crypsis, low population density, and frequent use of inaccessible habitats (Vine et al., 2009; Hughey et al., 2018). Indeed, for many species behaviour and its determinants remain poorly known, meaning that filling such knowledge gaps needs to be prioritised to comprehensively support scientific understanding, and in the case of at-risk species, as a foundation for conservation planning.

Reptiles have a variety of behavioural repertoires. Freshwater turtles, in particular, can exhibit behavioural shifts in response to environmental variation and its impact on hibernation, basking, or mating and nesting activities (Haxton and Berrill, 2001; Litzgus and Mousseau, 2004). The primary reproductive activities for turtles include finding suitable mates and nest sites, which can present substantive challenges, especially during the short seasonal window of activity in temperate regions or the higher risk of mortality while on land (Brown and Brooks, 1994; Steen et al., 2006). Gravid female turtles should be more active during the egg-laying period than non-gravid females or males as they search for suitable nest sites (Morreale et al., 1984) and gravid females may bask more than males to increase metabolic rates in support of egg development

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(Ross and Anderson, 1990; Krawchuk and Brooks, 1998). These expectations, however, are based on scant data on free-ranging turtles (but see Marchand et al., 2021) and nevertheless it remains unclear the extent to which gravid female turtles are more active than their counterparts and whether this is consistent across turtle species.

With the recent advent of miniaturised accelerometers and other sensors, it is now possible to track animal behaviour with a resolution and precision that far surpass traditional approaches involving direct observation or very high frequency (VHF) telemetry (e.g., Connoy et al., 2020; Kastle et al., 2021). Accelerometers are effective for tracking fine-scale behaviour and activity in turtles without interfering with their natural behaviour (Wilson et al., 2006; Brown et al., 2013; Auge et al., 2022). Here, we used accelerometers and water sensors to assess behavioural differences between reproductive groups in two free-ranging freshwater turtles (Blanding's turtles, *Emydoidea blandingii*; Painted turtles, *Chrysemys picta*) in the northern part of their range in southern Ontario, Canada. More specifically, we focused on behavioural differences between gravid females and non-gravid females. We expected that gravid females of both species would: 1) spend more time out of the water (basking) to increase metabolic rates associated with egg development; and 2) be more active on land during the nesting season (June), while they search for suitable nest sites. Our study is among the first efforts to use continuous-time data from accelerometry to track reproductive behaviour in free-ranging animals, and as such it provides insights into turtle behaviour that otherwise could not have been obtained using traditional monitoring methods.

Methods

Field methods. We studied Blanding's and Painted turtles in the South March Highlands in Ottawa, Ontario, Canada in the summers of 2018–2020. Both species have similar life history and habitat requirements, inhabit shallow ponds and marshes across eastern North America (Standing et al., 1999; Ernst and Lovich, 2009) and are syntopic within our study area. Both species spend considerable time basking or under water, and use terrestrial habitat to varying degrees when travelling between wetlands or searching for nest or overwintering sites (Hartwig and Kiviat, 2007). Due to prolonged snow cover during the winter months, turtles at northern latitudes overwinter for up to six months in aquatic sites, and consequently have a short active period during which they must acquire sufficient energy and thermal resources for digestion, growth and reproductive activities (Congdon, 1989; Edge et al., 2009). Blanding's and Painted turtles exhibit similar reproductive behaviours but differ in body and clutch size (Schwarzkopf and Brooks, 1985; Congdon and Loben Sels, 1991; Riley et al., 2011). In our study area, both species are near their northern range limit and emerge from hibernation in late April-early May, after which they engage in a variety of behaviours including mating and nesting activities, until the reproductive season ends in late June–early July (Congdon et al., 1983; Ernst and Lovich, 2009; Kastle et al., 2021).

We captured turtles during April–June via opportunistic hand capture and baited hoop-nets, and fitted them with a tri-axial accelerometer/water sensor data logger (model AxyTrek, Technosmart, Rome, Italy) and a VHF transmitter (model SI-2, Holohil, Carp, Canada) bolted to the marginal scutes of the carapace (9^{th} to 11^{th} scute) (Fig. 1). Both units combined weighed < 10% of turtle body mass. Data loggers recorded water conductivity and acceleration at 1 Hz (accelerometer: 10 bit resolution, $\pm 2\ g_{force}$), with acceleration and water sensor data being used to classify and validate activity states in each turtle species (Auge et al., 2022). We sexed turtles based on cloacal position and plastron concavity (Congdon and Loben Sels, 1991) and determined if females were gravid by manually palpating the inguinal region for oviductal eggs (Congdon et al., 1983) before being released at the capture site. During 2020 females were tracked using VHF-telemetry and recaptured in early June to confirm their gravidity status, as eggs are palpable closer to nesting season. Turtles were re-captured at the end of each summer to retrieve data loggers. All animals were handled in accordance with

Figure 1. Accelerometer (left) and VHF transmitter (right) attached to the rear carapace margin of a Painted turtle. Photo by Anne-Christine Auge.

guidelines from the Canadian Council on Animal Care and procedures were approved by the Trent University Animal Care Committee (Protocol No. 24729) and by the Ministry of Natural Resources and Forestry (MNRF, Permit No. KV-C-002-14).

Data analysis. We calculated overall dynamic body acceleration (ODBA) for each individual by summing dynamic acceleration in three body axes (Wilson et al., 2006; Gutowsky et al., 2016). We classified turtle activity states based on ODBA and water sensor thresholds: sitting in water, sitting on land, swimming, and walking (Auge et al., 2022), and calculated mean daily activity budgets for each individual. To test if activity states during the nesting season (June) differed between the three reproductive classes (males, gravid females, non-gravid females), we performed a permutational multivariate analysis of variance (PERMANOVA; with 999 permutations), based on Bray-Curtis similarity (Anderson, 2001, 2017; Tichagwa et al., 2020) using the *vegan* package (Oksanen et al., 2022) in R version 4.0.2 (R Development Core Team, Vienna, Austria, 2020). We considered mean proportion of time spent doing each of the four activities as the response variable, with reproductive class and species (and their interaction) as explanatory variables. When PERMANOVA detected significant differences, we further explored sources of variation via Kruskal-Wallis tests (Kruskal and Wallis, 1952) with Dunn's test for pairwise comparisons and adjusted p-values for multiple comparisons (Dunn, 1964; Dinno, 2015). We compared activity budgets between reproductive classes and species (Blanding's: gravid females $n = 4$, non-gravid females: $n = 3$, males: $n = 8$; Painted: gravid females $n = 6$, non-gravid females: $n = 9$, males: $n = 11$). Note that both Blanding's and Painted turtles in our study were synchronous in their nesting (A. Auge, unpublished data), allowing us to compare nesting behaviour across a consistent time period for both species.

Results

We determined the probability to detect gravidity rate, i.e. the proportion of female turtles confirmed to be gravid in June, but failing to have detectable eggs in May, to be 50% (A. Auge, unpublished data). This means that roughly half of the females captured and palpated for eggs before June in 2018 and 2019 ($n = 2$ Painted turtles), may have been falsely determined as 'non-gravid' (i.e., 4.5% of all sampled turtles).

Individual daily activity profiles throughout the season revealed distinct variation during pre-nesting and nesting seasons in both species, with gravid females spending more time sitting on land and walking compared to non-gravid females and males (Figs. 2, 3). Nesting activity differed by sex and reproductive status, but the magnitude of those differences varied by species (Table 1). Generally, activity differed between gravid females vs. males and non-gravid females, but were similar between males and non-gravid females (see Fig. 3, Tables 1, 2). Differences in activity between reproductive groups were less pronounced in Painted turtles compared to Blanding's turtles. In June, gravid female Blanding's turtles spent 23.3% and 25.1% less time during the day sitting in water, and 22.6% and 20.4% more time sitting on land compared to males and non-gravid females, respectively. Further, gravid Blanding's turtles spent 4.0% more time walking compared to both

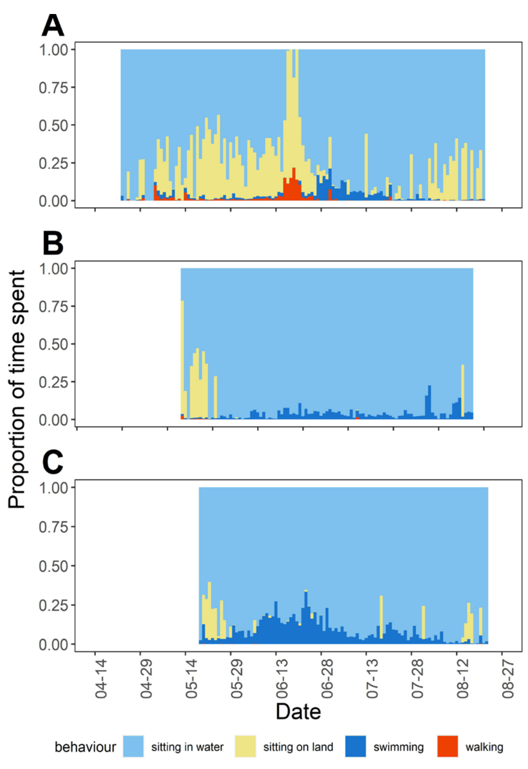

Figure 2. Sample turtle activity in the South March Highlands, Ottawa, ON, Canada. Examples of daily proportion of time spent with each of the four main activity states of a gravid female (A), a non-gravid female (B) and a male Blanding's turtle (C) throughout the active season 2019. Nesting behaviour (A) is associated with an increased time spent sitting on land and walking early in late May and June. Note that activity patterns were comparable in Painted turtles.

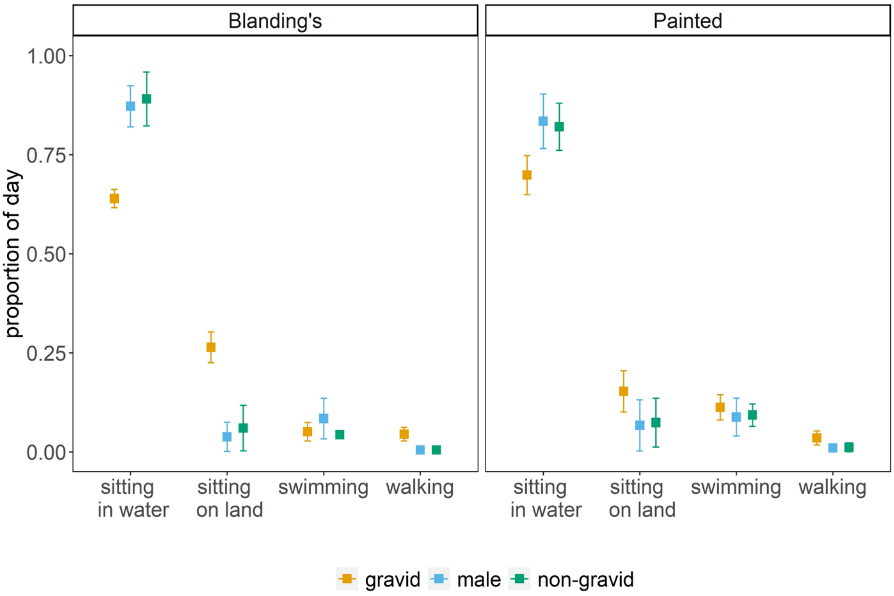

Figure 3. Activity across Blanding's and Painted turtle reproductive groups. Mean (±95% confidence interval) proportion of time spent with each activity of gravid female, non-gravid female and male freshwater turtles in the South March Highlands, Ottawa, ON, Canada during nesting month (June).

males and non-gravid females. All three reproductive groups spent a similar amount of time swimming (Fig. 3, Table 2). Likewise, gravid female Painted turtles spent 13.6% and 12.2% less time sitting in water, 8.6% and 7.9% more time sitting on land, and 2.5% and 2.0% more time walking compared to males and non-gravid females, respectively (Table 2). Similarly to Blanding's turtles, Painted turtle swimming activity did not differ across reproductive groups (Fig. 3, Table 2).

Discussion

Our study revealed activity differences during nesting season between gravid females and males and non-gravid females. Consistent with our expectations, gravid females spent more time sitting and walking on land and less time underwater compared to non-gravid females and males. We did not find any behavioural differences between males and non-gravid females, or between species.

The similarity in early-summer activity between males and non-gravid females, but their differences from gravid females, indicates that variation in freshwater turtle activity in this region is largely driven by reproductive processes and behaviours such as egg-development through increased basking behaviour and nest-site search through increased movement. This is supported by previous observations of increased frequency and duration of basking events in female compared to male freshwater turtles (Millar and Blouin-Demers, 2011; Markle and Chow-Fraser, 2014). Further, female turtles frequently move long distances to find suitable nest sites (Beaudry et al., 2010), and our results are consistent with other studies that demonstrate higher movement rates and (or) larger home ranges in gravid turtles compared to males (Aresco, 2005; Millar and

Table 1. Permutational multivariate analysis of variance (PERMANOVA) results showing differences in activity budgets (mean proportion of the day spent sitting in water, sitting on land, swimming and walking) between the sexes and reproductive classes (gravid females, non-gravid females, males) in the nesting month (June) for Blanding's and Painted turtles in the South March Highlands, Ottawa, ON, Canada.

Time	Parameter	D.f.	*F*-value	*p*-value
Nesting	Reproductive status	2	23.07	0.001
	Species	1	2.67	0.105
	Reproductive status x species	2	3.66	0.037
	Residuals	35		
	Total	40		

Table 2. Pairwise comparisons of activity states (mean proportion of the day spent sitting in water, sitting on land, swimming and walking) between turtle reproductive classes (gravid females, non-gravid females, males) for freshwater turtles in the South March Highlands, Ottawa, ON, Canada during the nesting month (June).

Species	Activity states	Reproductive classes compared		Mean % difference	95% CI	Adj. p-value
Blanding's	Sitting in water	Gravid	Male	23.29	15.16, 31.41	0.011
		Gravid	Non-gravid	25.14	15.00, 35.28	0.016
		Male	Non-gravid	1.86	-7.13, 10.84	0.440
	Sitting on land	Gravid	Male	-22.59	-29.37, -15.81	0.007
		Gravid	Non-gravid	-20.36	-28.82, -11.91	0.034
		Male	Non-gravid	2.23	-5.27, 9.72	0.381
	Swimming	Gravid	Male	3.29	-3.41, 10.00	0.177
		Gravid	Non-gravid	-0.79	-9.15, 7.56	0.366
		Male	Non-gravid	-4.09	-11.50, 3.32	0.217
	Walking	Gravid	Male	-3.99	-5.70, -2.28	0.008
		Gravid	Non-gravid	-4.01	-6.15, -1.87	0.027
		Male	Non-gravid	-0.02	-1.91, 1.87	0.440
Painted	Sitting in water	Gravid	Male	13.60	5.75, 21.44	0.002
		Gravid	Non-gravid	12.20	4.05, 20.34	0.004
		Male	Non-gravid	-1.40	-8.34, 5.55	0.357
	Sitting on land	Gravid	Male	-8.57	-16.32, -0.83	0.018
		Gravid	Non-gravid	-7.89	-15.93, 0.15	0.022
		Male	Non-gravid	0.69	-6.17, 7.54	0.388
	Swimming	Gravid	Male	-2.49	-7.40, 2.42	0.293
		Gravid	Non-gravid	-1.96	-7.06, 3.14	0.343
		Male	Non-gravid	0.53	-3.82, 4.88	0.277
	Walking	Gravid	Male	-2.53	-4.06, -1.00	0.009
		Gravid	Non-gravid	-2.35	-3.93, -0.76	0.013
		Male	Non-gravid	0.18	-1.17, 1.54	0.370

Blouin-Demers, 2011; Hamernick et al., 2020). Besides long-distance movement in search for nest sites, the accelerometer signature that we classified as "walking" likely also includes other similar movement patterns such as nest-digging, which can consist of up to 1.5 hours of terrestrial movement and exertion (Congdon and Gatten, 1989).

Few studies have characterised fine-scale and long-term behaviour in chelonians, with notable exceptions being research by Lagarde et al. (2008) and by Marchand et al. (2021) who used accelerometers to classify reproductive activities in tortoises and freshwater turtles, respectively. Specifically, Marchand et al. (2021) identified egg-laying behaviour via accelerometry, and our findings complement this work by clearly revealing behavioural differences in gravid female Blanding's and Painted turtles during the June nesting period. It follows that next steps in this research area should include investigating how individual differences in behaviour translate to variation in energetics, growth, survival, and productivity. Indeed, freshwater turtles do not readily invest in parental care after egg-laying, meaning that nesting behaviour, including nest site choice and construction, or time spent basking to support egg development, are the primary reproductive investments that may impact reproductive success and fitness (Pike, 2008). However, while increased terrestrial basking or activity may ultimately benefit reproductive success, such activity can also be deleterious by increasing adult female mortality risk from predation or vehicle collisions (Steen et al., 2006; Karson et al., 2018). In turn, lower adult female survival can contribute to skewed sex ratios, lower productivity and recruitment, and ultimately, population decline (Steen and Gibbs, 2004; Aresco, 2005, Auge et al., in review). Thus, investigating animal reproductive behaviour in natural settings is an important step for understanding population status and the determinants of population viability. It follows that such efforts can also inform conservation planning decisions for at-risk species, such as potential timing of road closures or predator control activities (Standing et al., 1999; Bowen et al., 2005). The advantage of using accelerometry for such investigations is that animals can be tracked continuously and non-invasively through time and space. This means that the usual gaps facing conventional time-budget datasets (e.g., lack of observations during nighttime or when animals cannot be readily detected or observed) can be overcome via effective use of accelerometry. Therefore, when accompanied by proper validation and behavioural classification (e.g., see Auge et al., 2022), accelerometry can provide a valuable tool for tracking the impacts of behaviour on animal populations (Fossette et al., 2012; Bernich et al., 2022).

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