



Compensating for Small Body Size: The Reproductive Ecology of Southern Spotted Turtle (*Clemmys guttata*) Populations

Authors: Chandler, Houston C., Stegenga, Benjamin S., and Mays, Jonathan D.

Source: Ichthyology & Herpetology, 110(2) : 268-277

Published By: The American Society of Ichthyologists and Herpetologists

URL: <https://doi.org/10.1643/h2021084>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Compensating for Small Body Size: The Reproductive Ecology of Southern Spotted Turtle (*Clemmys guttata*) Populations

Houston C. Chandler^{1,2}, Benjamin S. Stegenga¹, and Jonathan D. Mays³

Gradients in environmental conditions across a species' geographic distribution can drive variability in a variety of life history traits. In North American freshwater turtles, both body and clutch size have commonly been shown to vary latitudinally, and these two traits are often directly related, with larger individuals producing larger clutches. We studied the reproductive ecology in two Georgia populations of Spotted Turtles (*Clemmys guttata*) from 2016–2020 by attaching radio transmitters to female turtles during the breeding season. We x-rayed turtles to determine clutch sizes and used thread bobbins to locate nesting locations, allowing us to determine nest fates. Across all Spotted Turtle clutches ($n = 41$), mean clutch size was 2.1 (range: 1–4) eggs per clutch. Approximately 92% of individuals that we monitored produced at least one clutch during the breeding season, and we identified 16 instances of individuals producing more than one clutch in a single year, including six turtles triple clutching during 2018. We located 24 Spotted Turtle nests during the study, nine (37.5%) of which either hatched or partially hatched. The other nests were either depredated (41.7%), did not hatch due to infertility or environmental reasons (8.3%), or had an undetermined fate (12.5%). Our results indicate that annual reproductive output in southern Spotted Turtle populations can exceed that of northern populations where individuals produce a single larger clutch per reproductive season. Finally, opportunistic observations in Florida from 2014–2021 indicated that the reproductive season can begin over a month earlier than in southern Georgia, highlighting the variability in reproductive ecology even across a relatively short latitudinal distance.

VARIABILITY in life history traits can have important effects on several individual, population, and even ecosystem level processes (e.g., behavior, niche size, population size, and primary productivity; Bassar et al., 2010; Raffard et al., 2017). Furthermore, life history traits are broadly tied to evolutionary processes, providing much of the variability that selection can act upon and diversify (Bolnick et al., 2011). Intraspecific trait variation can be attributed to either genetic factors or to phenotypic plasticity resulting from variable environmental conditions (Schlichting, 1986; Gienapp et al., 2008; Moran et al., 2016). For species with wide geographic distributions or with distributions that span a gradient of environmental conditions, there may be significant differences in life history traits among populations (Berven and Gill, 1983; Miaud et al., 2000; Barbee et al., 2011; Williamson et al., 2016).

Latitudinal gradients have been widely recognized as a source of life history trait variability, both within and among species (Cardillo, 2002; Ashton and Feldman, 2003; Blanck and Lamouroux, 2007). Two traits that commonly vary across a latitudinal gradient are body size (i.e., Bergmann's Rule; Mayr, 1956) and clutch size, which are both generally predicted to decrease moving toward the equator (Iverson et al., 1993; Ashton and Feldman, 2003; Biancucci and Martin, 2010). Furthermore, body size and clutch size are directly related in a variety of taxa, with larger females producing larger clutches (Poulin, 1995; Shine and Seigel, 1996; Iverson and Moler, 1997; Ji et al., 1997; Barneche et al., 2018). However, there may also be relationships between either clutch size and egg size or egg size and body size in some taxa (Congdon and Gibbons, 1985; Elgar and Heaphy, 1989; Ford and Seigel, 1989), and larger eggs may provide long-term

benefits to offspring survival and reproduction (Segers and Taborsky, 2010; Krist, 2011). Thus, theory suggests that there is an optimal balance between clutch size and egg size (Smith and Fretwell, 1974; Brockelman, 1975; Parker and Begon, 1986; Bernardo, 1996), and the effects of intraspecific latitudinal variation in body size may play an important role in regulating these traits.

Reproductive output and its relationships to body size have been well studied in many North American turtles (Congdon and Gibbons, 1985; Iverson and Smith, 1993; Iverson et al., 1993; Litzgus and Mousseau, 2006; Lovich et al., 2018). For example, Congdon and Gibbons (1985) found a significant positive relationship between female body size and clutch size in four turtle species. Body size in turtles often increases with latitude (Ashton and Feldman, 2003), which can correspond to larger clutch sizes and sometimes larger eggs in northern turtle populations (Iverson and Smith, 1993; Iverson et al., 1993, 1997; Litzgus and Mousseau, 2006; Ryan and Lindeman, 2007). Furthermore, many turtle species are capable of producing multiple clutches during a single year (Iverson, 1977; Gibbons et al., 1982; McGuire et al., 2011). Multiple clutching boosts reproductive output and is a form of bet-hedging that spreads risk of reproductive failure across multiple clutches, both annually and within a female turtle's lifetime (Rollinson and Brooks, 2007; Lovich et al., 2015). However, multiple clutching can come at the expense of both clutch and egg size (Wilkinson and Gibbons, 2005; Ennen et al., 2017). The ability of female turtles to produce multiple clutches annually depends on the overall length of the breeding season and the environmental conditions that individuals experience (i.e., the energy available to devote to reproduction; Rollinson and Brooks, 2007; Lovich et al.,

¹ The Orianna Society, 11 Old Fruitstand Lane, Tiger, Georgia 30576; Email: (HCC) hchandler@oriannesociety.org. Send reprint requests to HCC.

² Department of Fish and Wildlife Conservation, Virginia Tech, 310 West Campus Drive, Blacksburg, Virginia 24061.

³ Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 1105 SW Williston Road, Gainesville, Florida 32601. Submitted: 30 June 2021. Accepted: 23 October 2021. Associate Editor: D. S. Siegel.

© 2022 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/h2021084 Published online: 17 May 2022

2015), although the effects of body condition on clutch frequency may only manifest over multiple breeding seasons (Litzgus et al., 2008).

Spotted Turtles (*Clemmys guttata*) are one of the smallest turtles in North America, with adults reaching maturity at approximately 80–100 mm midline carapace length (CL; Iverson and Lewis, 2018), depending on the population (Ernst and Lovich, 2009). Spotted Turtles have a broad latitudinal distribution that stretches from southern Canada and the Great Lakes Region to northern Florida in the southeastern United States. However, Spotted Turtle populations are broadly considered to be declining across much of their range (van Dijk, 2011; COSEWIC, 2014). Populations inhabit a variety of wetland types and experience significantly different environmental conditions along a latitudinal gradient, including much longer activity seasons in the southern portion of the distribution (Ernst, 1976, 1982; Lovich, 1988; Litzgus and Brooks, 1998; Litzgus and Mousseau, 2004; Chandler et al., 2020). In southern populations, the breeding season can begin over a month earlier than in populations restricted by a colder winter and spring (Litzgus and Brooks, 1998; Litzgus and Mousseau, 2003). Unsurprisingly, studies have reported that both adult body size and clutch size can vary latitudinally in Spotted Turtles, with larger individuals and clutches present in northern populations (Litzgus et al., 2004; Litzgus and Mousseau, 2006).

Litzgus and Mousseau (2003) reported five instances of female Spotted Turtles producing multiple clutches (including one individual that triple clutched) during a single breeding season in a South Carolina population. Multiple clutching in southern Spotted Turtle populations may offset differences in clutch sizes among populations, resulting in an overall similar annual reproductive output between southern and northern populations (Litzgus and Mousseau, 2006). However, no additional research has attempted to quantify if multiple clutching is common throughout the southern portion of the Spotted Turtle's range. Here, we present reproductive data collected from two Spotted Turtle populations in the Coastal Plain of southeastern Georgia, and we also discuss opportunistic observations collected in two Florida populations as part of a long-term monitoring project. The goals of our study were to 1) monitor the timing of the breeding season in Georgia and Florida populations, 2) quantify clutch sizes, 3) identify the frequency of multiple clutching, and 4) measure nest survival rates. We hypothesized that clutch sizes would be generally small in these populations but that female turtles would frequently produce multiple clutches during a single breeding season because of the long active season and associated resources.

MATERIALS AND METHODS

Study sites.—We studied two Spotted Turtle populations located in the Coastal Plain of southeastern Georgia and two populations in northern Florida (specific locations are withheld throughout because of collecting concerns; Fig. 1). The Georgia sites are composed of relatively small wetland complexes associated with nearby streams. The wetlands at one site include both natural (floodplain and beaver wetlands) and artificial (ditches) wetlands, while the other site is composed completely of floodplain forests. Sites are located approximately 145 km apart, and a more detailed

description of site characteristics can be found in Chandler et al. (2019, 2020). The two sites in Florida are located approximately 50 km apart and 250 km south of the nearest Georgia site (Fig. 1). Florida sites consist of shallow water pools with thick detritus-muck soils embedded in large swamp and floodplain complexes that are fed and drained by small, low-gradient streams. One site is predominated by cypress-gum swamp with peripheral pockets of mixed hardwoods (e.g., Red Maple [*Acer rubrum*] and Sweetbay Magnolia [*Magnolia virginiana*]) and Loblolly Pine (*Pinus taeda*), while the other site is mesic floodplain forest that included both mixed hardwoods (e.g., Red Maple and Swamp Chestnut Oak [*Quercus michauxii*]) and pine flatwoods. Both Florida sites, now in various stages of restoration, have a long-standing history of forestry, turpentine, indigo, and/or wild rice production, all of which modified the natural hydrology to varying extents via ditching, bedding silviculture practices, and digging canals.

Data collection.—In Georgia, we assessed fecundity as part of ongoing population monitoring, and data collection was divided across three years (2016, 2018, and 2020). In all years, we captured female Spotted Turtles through a combination of trapping and visual encounter surveys during the beginning of the active season (March–April). Because of various logistical and project constraints, the exact data collected differed across years, so we describe each year separately below.

In 2016, we collected all female turtles involved in a radio telemetry project (Chandler et al., 2019) and had them x-rayed at the Georgia Sea Turtle Center on 11 May. We used radiographs as our primary method to identify clutch sizes throughout this project (Gibbons and Greene, 1979). We based the timing of these x-rays on previously published estimates of when Spotted Turtles were likely to be gravid in the Southeast (Litzgus and Mousseau, 2003). We returned all turtles to their point of capture within 24 hours, and this was the only reproductive data collected in 2016.

In 2018, we initiated surveys to quantify multiple aspects of the Spotted Turtle reproductive cycle. During routine population monitoring, we attached 5.0 g radio transmitters (Model: SOPR-2190, Wildlife Materials International, Inc., Murphysboro, IL) to the carapace of adult female turtles ($n = 17$; midline CLs ranged from 91.9–111.5 mm) using a water proof epoxy (J-B Weld-WaterWeld, Atlanta, GA, USA). We attached transmitters on the day of capture and released turtles at their capture location within a few hours. Once radio transmitters had been attached to female turtles, we located turtles once a week to check for signs of gravidity. We weighed each turtle each time it was located and palpated turtles by inserting a finger into the inguinal shell cavity, anterior to the hind legs. The small size of Spotted Turtles in these populations makes them challenging to effectively palpate, and palpation is not 100% accurate in turtles (Keller, 1998). However, we were regularly able to detect shelled eggs using this approach in most individuals.

When we confirmed that some turtles were gravid by a combination of weight gain and palpation, we captured all turtles and had them x-rayed at the Georgia Sea Turtle Center to accurately measure clutch sizes. We released all turtles at their point of capture within 12 hours. For turtles that were confirmed gravid, we increased the frequency of tracking to every day or every other day, depending on the weather and

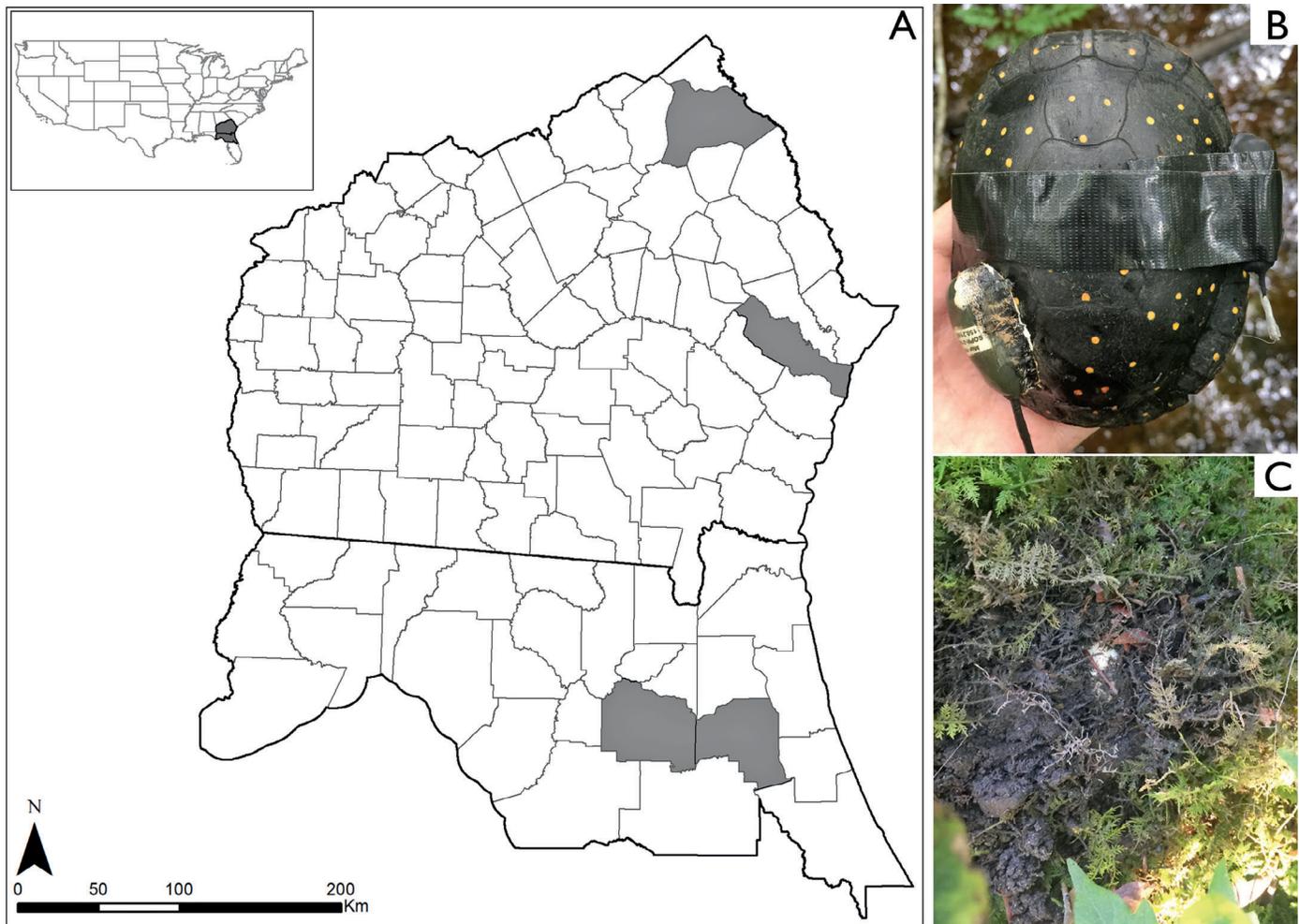


Fig. 1. Reproductive ecology was monitored in four Spotted Turtle (*Clemmys guttata*) populations spread across southeastern Georgia and northern Florida from 2014–2021 (A). In Georgia, female Spotted Turtles were tracked to nesting locations using a combination of radio telemetry and thread bobbins (B). Nests were laid in a variety of substrates, including loose soils and leaf litter, sphagnum moss clumps, and rotten logs, and female turtles failed to completely cover eggs on multiple occasions (C).

staff availability. To locate nesting sites, we attached cocoon thread bobbins to each gravid turtle, allowing us to precisely follow turtle movements since the previous tracking event (Breder, 1927). Thread bobbins were wrapped in plastic wrap and dipped in Plasti Dip (Plasti Dip, Blaine, MN, USA) so that only the end of the thread was exposed to the elements (Knoerr et al., 2021). We initially attached the waterproofed thread bobbins opposite the radio transmitters using a quick drying epoxy but ultimately decided that repeatedly changing the thread bobbins was causing too much wear on the turtle's shells. We therefore switched to attaching thread bobbins using a small loop of black duct or electrical tape wrapped around the center of the turtle's shell (Fig. 1). Regardless of attachment method, we tied the loose end of the thread bobbin to a small tree and released the turtle near the capture location.

After a thread bobbin was attached, we checked turtles every 24–48 hours. We replaced thread bobbins each time we located a turtle unless the turtle had moved only a few meters from its previous location. We used a combination of weight loss and palpation to determine when female turtles had nested (i.e., usually a drop in weight of at least 10 g occurred overnight). If we suspected that a turtle had

nested since the previous check, we removed the thread bobbin from the turtle and followed the thread trail, looking for any signs that the thread passed through a suitable nesting substrate. We recorded the location, a general description of the nest placement (e.g., substrate and whether eggs were visible to the observer), and the surrounding habitat of all identified nests. We estimated the canopy cover at nest sites using a convex spherical densiometer (Lemon, 1956) and measured the distance to the nearest water.

We checked all nests every 2–3 weeks to determine nest fates. We classified each nest as either hatched, unhatched, or depredated. Nests that were depredated were generally completely dug up with little or no sign of egg shells remaining in or around the nest chamber. Unhatched nests had eggs remaining in them well after other nests had hatched, and these eggs had often begun to mold or deform. We classified nests as hatched if there was minimal sign of disturbance around the nest and if mostly intact egg shells remained in or near the nest chamber. We opportunistically deployed game cameras on a subset of nests to document predation events. We repeated the entire procedure (i.e., x-raying to check for gravidity, thread tracking, and checking

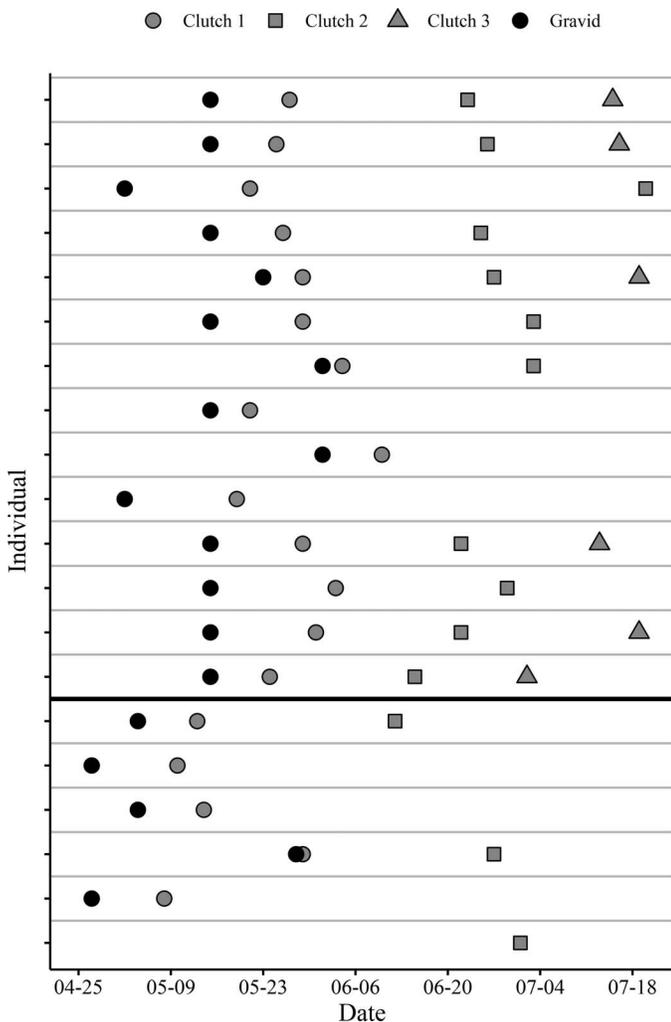


Fig. 3. Timing of Spotted Turtle (*Clemmys guttata*) nesting events at two sites in Georgia during 2018 (above black line) and 2020 (below black line). The first time turtles were identified as gravid (determined by a combination of x-rays and palpation) is indicated by black circles.

produced multiple clutches (83% of individuals that reproduced at least once, excluding one turtle that was added to the study after first clutches were laid). We documented double clutching in all five individuals that produced multiple clutches in 2020 but were unable to identify if any of these turtles produced a third clutch because of logistical constraints (see above). Clutch size was significantly impacted by clutch number ($F_{2,22} = 4.2$, $P = 0.03$), with third (mean = 1.5 ± 0.6 [SD]) clutches being significantly smaller, on average, than either first (mean = 2.1 ± 0.7 [SD]) or second (mean = 2.2 ± 0.8 [SD]) clutches ($P = 0.04$ and 0.03 , respectively; Fig. 2). There was no effect of female body size on the number of eggs per clutch ($F_{1,18} = 0.02$, $P = 0.90$), although body size was positively correlated with the total number of clutches laid during 2018 ($r = 0.57$). For individuals that triple clutched, the total number of eggs produced per year (i.e., total annual reproductive output) by the three individuals where all three clutch sizes were identified ranged from 5–7 eggs. The three other turtles with at least one unknown clutch size produced approximately 6–8 eggs during a single breeding season (assuming a mean

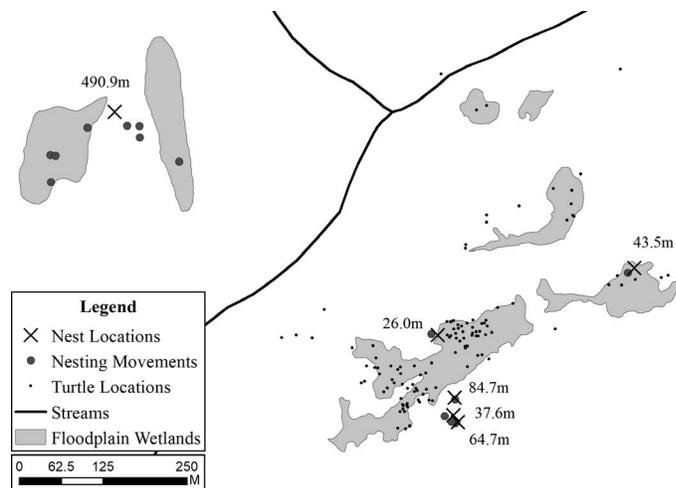


Fig. 4. Spotted Turtle (*Clemmys guttata*) nesting locations and approximate distance from normal activity areas to nesting locations from a population in southeastern Georgia. Nesting movements were defined by movements out of a turtle's normal activity area followed by nesting and immediate return to the normal activity area.

clutch size of two eggs for unknown clutches). Individuals that double clutched produced 2–5 eggs per year.

From 2014–2021, we observed 18 instances of gravid female Spotted Turtles in Florida (approximately 38% of the occasions that a female turtle was palpated from March through May). Gravid turtles were identified from 22 March through 8 May (six times in March, nine times in April, and three times in May). A single gravid female was x-rayed on 29 March 2019 and determined to have three shelled eggs.

Nesting.—In the Georgia populations, we located a total of 16 and 8 nests during 2018 and 2020, respectively (approximately 50% of the total nests laid by turtles included in the study). Across both years, nesting dates ranged from 8 May through 10 June for the first clutch, 12 June through 20 July for the second clutch (2 July if excluding a single individual that laid a second observed clutch on 20 July), and 2 July through 19 July for the third clutch (Fig. 3). Of the 24 nests that we monitored, nine either hatched or partially hatched (37.5%), producing a total of 17 hatchling Spotted Turtles. The remaining nests were either depredated (41.7%), did not hatch because of other factors (8.3%), or experienced an unknown fate (12.5%). Observed nest predators included Nine-banded Armadillos (*Dasypus novemcinctus*) and Raccoons (*Procyon lotor*).

Nests were typically constructed on the periphery of wetlands, with turtles sometimes traveling into adjacent habitats to lay eggs (Fig. 4). On average, female turtles moved approximately 97.5 m (range: 1.5–490.9 m; $n = 20$) from their previous locations to reach nesting locations. We observed several instances of relatively long-distance movements that culminated in nesting before turtles returned to their typical activity areas (Fig. 4). Of the 24 identified nests, only six (25%) were laid within the MCP formed by all non-nesting telemetry observations for that individual. Despite moving away from typical activity areas, Spotted Turtle nests were, on average, within 5 m of flooded areas, although the distance to water typically increased as wetlands dried over the summer. Nesting locations were characterized by areas of high canopy cover (mean = 88%, range: 6.7–100%). Spotted

Table 1. Nest ($n = 8$) and egg ($n = 13$) measurements recorded from Spotted Turtle (*Clemmys guttata*) nests at a single site in Georgia during 2020.

	Nest depth (mm)	Nest width (mm)	Egg length (mm)	Egg width (mm)	Egg mass (g)
Mean	53.9	42.4	33.2	17.2	6.2
Standard deviation	8.2	13.2	2.4	1.0	1.3
Min	51	22	28.5	15.9	4
Max	67	59	37.7	19.2	9

Turtles dug small nest chambers (Table 1) in a variety of substrates, including loose soil and leaf litter, sphagnum moss clumps, rotting logs, and raised hummocks containing thick grass clumps. On three occasions turtles failed to completely cover eggs after they were laid (Fig. 1). Eggs measured in Georgia during 2020 had a mean length of 33.2 mm and a mean width of 17.2 mm (Table 1).

DISCUSSION

Our results indicate that annual reproductive output in Georgia Spotted Turtle populations is characterized by a majority of females reproducing (over 90% of individuals included in our study reproduced at least once) and frequent multiple clutching. This includes six instances of triple clutching, expanding on previous observations of this reproductive capability in South Carolina (Litzgus and Mousseau, 2003). This type of reproductive strategy has also been documented in other small, freshwater turtle species from the southeastern United States (Iverson, 1977; Gibbons, 1983). We therefore suggest that multiple clutching, including triple clutching, is likely a common life history adaptation throughout the southern portion of the Spotted Turtle's distribution because of long periods of suitable environmental conditions that allow adult turtles to lay multiple clutches and allow nests laid later in the summer to hatch before cooler temperatures arrive in the late fall (Chandler et al., 2020).

Previous studies have indicated that clutch size declines with latitude in both Spotted Turtles (Litzgus and Mousseau, 2006) and other turtle species (Iverson et al., 1993; Ashton and Feldman, 2003; Lovich et al., 2018). Our results are consistent with this trend, and the overall estimate of 2.1 eggs per clutch is the smallest reported average clutch size for any Spotted Turtle population. This includes eight instances of females producing only a single egg, which to our knowledge has not been previously documented in wild Spotted Turtles. The mean midline CL of female turtles included in our study was 99.6 mm, which is smaller than females from South Carolina (mean midline CL = 103.8 mm; Litzgus and Mousseau, 2004) and many but not all northern populations (mean midline CL range: 92.4–115.0 mm; Litzgus and Brooks, 1998). Thus, small body size in the Georgia populations likely limits the ability of individuals to produce either larger clutches (must fit inside the body cavity; Ryan and Lindeman, 2007) or larger eggs (must pass through the pelvic girdle). Furthermore, we found a negative effect of clutch number on clutch size, and triple clutching likely has a significant energetic cost that could impact both clutch size and egg size (Ennen et al., 2017). We lacked the sample size to examine differences in egg size across clutches or female body sizes, but eggs measured in 2020 were generally similar in size to those reported from other Spotted Turtle populations (Litzgus and Mousseau, 2006). Our results

indicate that multiple clutching represents an important adaptation for southern Spotted Turtle populations that can potentially compensate for small body sizes by increasing the overall annual reproductive output to a similar or even higher level than what is observed in northern populations with larger individuals (Litzgus and Brooks, 1998). Overall, multiple clutching is a fairly common adaptation in a variety of taxa (Emlen, 1977; Vitt, 1977; Breihagen, 1988) and potentially has benefits that extend beyond a simple increase in annual reproductive output (e.g., spreading risk of reproductive failure spatially and temporally across multiple clutches; Schwarz and Meiri, 2017).

Spotted Turtles in Georgia developed and laid multiple clutches over an approximately three-month period from May to July, and timing was similar to that reported by Litzgus and Mousseau (2003) in South Carolina. Our data suggest that there is some variability in the timing of this reproductive period, both among years and individuals. For example, first clutches in 2020 were laid approximately ten days earlier than in 2018. This inter-annual variation is likely driven by differences in environmental conditions, which could impact when female turtles begin developing eggs (Lovich et al., 2012, 2017; Mitchell et al., 2017). Within years, the timing of nesting for each clutch number was spread across an approximately 2–4-week period for all individuals (i.e., the difference in time between the first and last nesting event for each clutch number). It is unclear what factors drive this variability within populations, but it may be related to individual body condition or resource allocation, which can also impact clutch frequency (Bêty et al., 2003; Rollinson and Brooks, 2007, 2008; Litzgus et al., 2008).

Although our data from Florida are limited in scope, they indicate a significantly earlier start to the reproductive period than was observed in either Georgia or South Carolina. Furthermore, no evidence of gravid turtles was found after early May despite several individuals being routinely monitored during a multi-year telemetry study (Mays, unpubl. data). The two Florida sites are approximately 250 km south (approximately 2.2° of latitude) of the closest site in Georgia, while the sites in Georgia were separated by approximately 145 km (approximately 1.2° of latitude). This earlier start to the reproductive period is likely driven by milder winters in Florida. Across both Georgia and Florida, we detected no evidence that Spotted Turtles reproduce outside of March–July. However, other freshwater turtle species in the Southeast have been observed nesting in all 12 months of the year (Wilson et al., 1999), and Spotted Turtles in southern populations do exhibit courtship and mating behavior during the fall (Litzgus and Mousseau, 2006; Chandler et al., 2019). Given the challenges associated with monitoring Spotted Turtles in the Southeast (e.g., low detectability, long reproductive seasons, and long periods of dry wetlands), it would not be surprising to document additional reproductive

behaviors occurring outside of the timeframe noted in our study.

Of the 24 nests that we monitored, approximately 50% did not hatch because of predation or other factors (we suspect that two of the three nests with unknown fates were also depredated). Data on nesting success rates for Spotted Turtle populations are scarce. Of the six nests located in Maine by Beaudry et al. (2010), 67% did not hatch but only one was depredated, and in Pennsylvania, Ernst (1970) reported that 18 of 43 monitored eggs (42%) did not hatch. Litzgus and Brooks (1998) found that all three monitored nests were depredated, including two by ants. Overall, these predation rates are lower than have been observed in some other turtle species (Butler et al., 2004; Knoerr et al., 2021), although there is likely significant, currently undocumented, variation across Spotted Turtle populations. Overall, it appears that nests in both Georgia populations commonly produce hatchling turtles, and both hatchling and sub-adult turtles have been observed during population monitoring at these sites (Chandler, unpubl. data). However, more research is needed to better understand survivorship of hatchling and juvenile turtles and whether spreading risk across multiple clutches ultimately influences reproductive success and population dynamics in southern populations.

Spotted Turtles frequently moved outside of their normal activity areas in search of nesting habitat, sometimes traveling several hundred meters over a period of a few days. Nesting locations were characterized by high canopy cover, and nests were frequently laid partially under herbaceous or shrubby vegetation, which may be important to protect shallow nests from high temperatures in the Southeast (Wilson, 1998; Litzgus and Mousseau, 2006). Unlike in some other populations (Beaudry et al., 2010), we observed no evidence of Spotted Turtles nesting in anthropogenic habitats even though they were present at both sites. Observations of Spotted Turtles moving long distances (sometimes across uplands), moving into the periphery of wetlands, and traveling to otherwise unused parts of wetland complexes suggest that for habitat protection to be successful it must include the larger wetland complex as well as a terrestrial buffer to preserve nesting habitats and travel corridors (Burke and Gibbons, 1995; Joyal et al., 2001).

The results of our work have implications for future studies attempting to understand population dynamics of Spotted Turtle populations in the southern portion of their range. Our results and those of Litzgus and Mousseau (2006) strongly indicate that estimating fecundity in southern populations using parameters measured at different latitudes would be inappropriate. Turtle life histories are broadly reliant on high adult survival, and reducing adult survival has been shown to negatively impact Spotted Turtle populations (Enneson and Litzgus, 2008, 2009; Howell and Seigel, 2019). However, a high percentage of females reproducing annually combined with frequent multiple clutching that produces more eggs per year and spreads mortality risk across multiple reproductive events could make southern populations more resilient to changes in the environment that impact other life stages. Future work should attempt to better understand the population dynamics of southern populations to test this hypothesis and examine how environmental stochasticity influences reproductive output. Finally, Spotted Turtles display temperature-dependent sex determination (Ewert et al., 2004), and

research is needed to understand the effects of climate change on sex ratios and population dynamics, especially in southern populations where environmental temperatures are higher than those experienced by northern populations.

DATA ACCESSIBILITY

Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

ACKNOWLEDGMENTS

We thank S. Baxter-Bray, W. Baxter-Bray, J. Bolton, Z. Cava, B. Chandler, A. Greene, H. Hall, B. Harris, M. Holden, C. Jenkins, M. Knoerr, J. Litzgus, L. Mailler, P. Moler, T. Norton, R. Sommer, S. Stowell, C. Thompson, B. Tornwall, B. Williams, and L. Williams for their assistance with this project. Spotted Turtle research in Georgia was initiated by D. Stevenson. The manuscript was improved by comments from J. Baron, G. Brooks, N. Caruso, C. Haas, and M. Holden. The Georgia Department of Natural Resources (DNR), Georgia Sea Turtle Center, and Oatland Island Wildlife Center provided logistical assistance. The project was funded by the U.S. Fish and Wildlife Service (Cooperative Agreement Award F15AC00965). Georgia research was carried out under Georgia DNR Scientific Collecting Permits numbers 29-WJH-16-21, 115579244, 353660973, and 119101898, and Florida work was carried out by Florida Fish and Wildlife Conservation Commission staff.

LITERATURE CITED

- Ashton, K. G., and C. R. Feldman. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57:1151–1163.
- Barbee, N. C., R. Hale, J. Morrongiello, A. Hicks, D. Semmens, B. J. Downes, and S. E. Swearer. 2011. Large-scale variation in life history traits of the widespread diadromous fish, *Galaxias maculatus*, reflects geographic differences in local environmental conditions. *Marine and Freshwater Research* 62:790–800.
- Barneche, D. R., D. R. Robertson, C. R. White, and D. J. Marshall. 2018. Fish reproductive-energy output increases disproportionately with body size. *Science* 360:642–645.
- Bassar, R. D., M. C. Marshall, A. López-Sepulcre, E. Zandonà, S. K. Auer, J. Travis, C. M. Pringle, A. S. Flecker, S. A. Thomas, D. F. Fraser, and D. N. Reznick. 2010. Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences of the United States of America* 107:3616–3621.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Beaudry, F., P. G. DeMaynadier, and M. L. Hunter Jr. 2010. Nesting movements and the use of anthropogenic nesting sites by Spotted Turtles (*Clemmys guttata*) and Blanding's

- Turtles (*Emydoidea blandingii*). *Herpetological Conservation and Biology* 5:1–8.
- Bernardo, J.** 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *American Zoologist* 36:216–236.
- Berven, K. A., and D. E. Gill.** 1983. Interpreting geographic variation in life-history traits. *American Zoologist* 23:85–97.
- Bêty, J., G. Gauthier, and J. Giroux.** 2003. Body condition, migration, and timing of reproduction in Snow Geese: a test of the condition-dependent model of optimal clutch size. *The American Naturalist* 162:110–121.
- Biancucci, L., and T. E. Martin.** 2010. Can selection on nest size from nest predation explain the latitudinal gradient in clutch size? *Journal of Animal Ecology* 79:1086–1092.
- Blanck, A., and N. Lamouroux.** 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. *Journal of Biogeography* 34:862–875.
- Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur.** 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* 26:183–192.
- Breder, R. B.** 1927. Turtle trailing: a new technique for studying the life habits of certain Testudinata. *Zoologica* 9: 231–243.
- Breihagen, T.** 1988. Nesting biology and mating system in an alpine population of Temminck's Stint *Calidris temminckii*. *Ibis* 131:389–402.
- Brockelman, W. Y.** 1975. Competition, the fitness of offspring, and optimal clutch size. *The American Naturalist* 109:677–699.
- Burke, V. J., and J. W. Gibbons.** 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina bay. *Conservation Biology* 9:1365–1369.
- Butler, J. A., C. Broadhurst, M. Green, and Z. Mullin.** 2004. Nesting, nest predation, and hatchling emergence of the Carolina Diamondback Terrapin, *Malaclemys terrapin centrata* in northeastern Florida. *The American Midland Naturalist* 152:145–155.
- Calenge, C.** 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Cardillo, M.** 2002. The life-history basis of latitudinal diversity gradients: How do species traits vary from the poles to the equator? *Journal of Animal Ecology* 71:79–87.
- Chandler, H. C., B. S. Stegenga, and D. J. Stevenson.** 2019. Movement and space use in southern populations of Spotted Turtles (*Clemmys guttata*). *Southeastern Naturalist* 18:602–618.
- Chandler, H. C., B. S. Stegenga, and D. J. Stevenson.** 2020. Thermal ecology of Spotted Turtles (*Clemmys guttata*) in two southern populations. *Copeia* 108:737–745.
- Congdon, J. D., and J. W. Gibbons.** 1985. Egg components and reproductive characteristics of turtles: relationships to body size. *Herpetologica* 41:194–205.
- COSEWIC.** 2014. COSEWIC assessment and status report on the Spotted Turtle *Clemmys guttata* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada.
- Elgar, M. A., and L. J. Heaphy.** 1989. Covariation between clutch size, egg weight and egg shape: comparative evidence for chelonians. *Journal of Zoology* 219:137–152.
- Emlen, S. T.** 1977. “Double Clutching” and its possible significance in the Bullfrog. *Copeia* 1977:749–751.
- Ennen, J. R., J. E. Lovich, R. C. Averill-Murray, C. B. Yackulic, M. Agha, C. Loughran, L. Tennant, and B. Sinervo.** 2017. The evolution of different maternal investment strategies in two closely related desert vertebrates. *Ecology and Evolution* 7:3177–3189.
- Enneson, J. J., and J. D. Litzgus.** 2008. Using long-term data and a stage-classified matrix to assess conservation strategies for an endangered turtle (*Clemmys guttata*). *Biological Conservation* 141:1560–1568.
- Enneson, J. J., and J. D. Litzgus.** 2009. Stochastic and spatially explicit population viability analyses for an endangered freshwater turtle, *Clemmys guttata*. *Canadian Journal of Zoology* 87:1241–1254.
- Ernst, C. H.** 1970. Reproduction in *Clemmys guttata*. *Herpetologica* 26:228–232.
- Ernst, C. H.** 1976. Ecology of the Spotted Turtle, *Clemmys guttata* (Reptilia, Testudines, Testudinidae), in southeastern Pennsylvania. *Journal of Herpetology* 10:25–33.
- Ernst, C. H.** 1982. Environmental temperatures and activities in wild Spotted Turtles, *Clemmys guttata*. *Journal of Herpetology* 16:112–120.
- Ernst, C. H., and J. E. Lovich.** 2009. Turtles of the United States and Canada. Second edition. Johns Hopkins University Press, Baltimore, Maryland.
- Ewert, M. A., C. R. Etchberger, and C. E. Nelson.** 2004. Turtle sex-determining modes and TSD patterns, and some TSD pattern correlates, p. 21–32. *In: Temperature-Dependent Sex Determination in Vertebrates*. N. Valenzuela and V. A. Lance (eds.). Smithsonian Institution Press, Washington, D.C.
- Ford, N. B., and R. A. Seigel.** 1989. Relationships among body size, clutch size, and egg size in three species of oviparous snakes. *Herpetologica* 45:75–83.
- Gibbons, J. W.** 1983. Reproductive characteristics and ecology of the Mud Turtle, *Kinosternon subrubrum* (Lacépède). *Herpetologica* 39:254–271.
- Gibbons, J. W., and J. L. Greene.** 1979. X-ray photography: a technique to determine reproductive patterns of freshwater turtles. *Herpetologica* 35:86–89.
- Gibbons, J. W., J. L. Greene, and K. K. Patterson.** 1982. Variation in reproductive characteristics of aquatic turtles. *Copeia* 1982:776–784.
- Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merilä.** 2008. Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology* 17:167–178.
- Howell, H. J., and R. A. Seigel.** 2019. The effects of road mortality on small, isolated turtle populations. *Journal of Herpetology* 53:39–46.
- Iverson, J. B.** 1977. Reproduction in freshwater and terrestrial turtles of North Florida. *Herpetologica* 33:205–212.
- Iverson, J. B., C. P. Balgooyen, K. K. Byrd, and K. K. Lyddan.** 1993. Latitudinal variation in egg and clutch size in turtles. *Canadian Journal of Zoology* 71:2448–2461.
- Iverson, J. B., H. Higgins, A. Sirulnik, and C. Griffiths.** 1997. Local and geographic variation in the reproductive

- biology of the Snapping Turtle (*Chelydra serpentina*). *Herpetologica* 53:96–117.
- Iverson, J. B., and E. L. Lewis. 2018. How to measure a turtle. *Herpetological Review* 49:453–460.
- Iverson, J. B., and P. E. Moler. 1997. The female reproductive cycle of the Florida Softshell Turtle (*Apalone ferox*). *Journal of Herpetology* 31:399–409.
- Iverson, J. B., and G. R. Smith. 1993. Reproductive ecology of the Painted Turtle (*Chrysemys picta*) in the Nebraska Sandhills and across its range. *Copeia* 1993:1–21.
- Ji, X., Y. Xie, P. Sun, and X. Zheng. 1997. Sexual dimorphism and female reproduction in a viviparous snake, *Elaphe rufodorsata*. *Journal of Herpetology* 31:420–422.
- Joyal, L. A., M. McCollough, and M. L. Hunter Jr. 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. *Conservation Biology* 15:1755–1762.
- Keller, C. 1998. Assessment of reproductive state in the turtle *Mauremys leprosa*: a comparison between inguinal palpation and radiography. *Wildlife Research* 25:527–531.
- Knoerr, M. D., G. J. Graeter, and K. Barrett. 2021. Hatch success and recruitment patterns of the Bog Turtle. *The Journal of Wildlife Management* 85:293–302.
- Krist, M. 2011. Egg size and offspring quality: a meta-analysis in birds. *Biological Reviews* 86:692–716.
- Lemon, P. E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science* 2:314–320.
- Litzgus, J. D., F. Bolton, and A. I. Schulte-Hostedde. 2008. Reproductive output depends on body condition in Spotted Turtles (*Clemmys guttata*). *Copeia* 2008:86–92.
- Litzgus, J. D., and R. J. Brooks. 1998. Growth in a cold environment: body size and sexual maturity in a northern population of Spotted Turtles, *Clemmys guttata*. *Canadian Journal of Zoology* 76:773–782.
- Litzgus, J. D., S. E. DuRant, and T. A. Mousseau. 2004. Clinal variation in body and cell size in a widely distributed vertebrate ectotherm. *Oecologia* 140:551–558.
- Litzgus, J. D., and T. A. Mousseau. 2003. Multiple clutching in Spotted Turtles, *Clemmys guttata*. *Journal of Herpetology* 37:17–23.
- Litzgus, J. D., and T. A. Mousseau. 2004. Home range and seasonal activity of southern Spotted Turtles (*Clemmys guttata*): implications for management. *Copeia* 2004:804–817.
- Litzgus, J. D., and T. A. Mousseau. 2006. Geographic variation in reproduction in a freshwater turtle (*Clemmys guttata*). *Herpetologica* 62:132–140.
- Lovich, J. E. 1988. Geographic variation in the seasonal activity cycle of Spotted Turtles, *Clemmys guttata*. *Journal of Herpetology* 22:482–485.
- Lovich, J. E., M. Agha, M. Meulblok, K. Meyer, J. Ennen, C. Loughran, S. V. Madrak, and C. Bjurlin. 2012. Climatic variation affects clutch phenology in Agassiz's Desert Tortoise (*Gopherus agassizii*). *Endangered Species Research* 19:63–74.
- Lovich, J. E., R. C. Averill-Murray, M. Agha, J. R. Ennen, and M. Austin. 2017. Variation in annual clutch phenology of Sonoran desert tortoises (*Gopherus morafkai*) in central Arizona. *Herpetologica* 73:313–322.
- Lovich, J. E., J. R. Ennen, C. B. Yackulic, K. Meyer-Wilkins, M. Agha, C. Loughran, C. Bjurlin, M. Austin, and S. Madrak. 2015. Not putting all their eggs in one basket: bet-hedging despite extraordinary annual reproductive output of desert tortoises. *Biological Journal of the Linnean Society* 115:399–410.
- Lovich, J. E., J. W. Gibbons, and K. Green. 2018. Life history with emphasis on geographic variation, p. 63–80. *In: Ecology and Conservation of the Diamondback Terrapin Malaclemys terrapin*. W. M. Roosenburg and V. S. Kennedy (eds.). Johns Hopkins University Press, Baltimore, Maryland.
- Mayr, E. 1956. Geographical character gradients and climatic adaptations. *Evolution* 10:105–108.
- McGuire, J. M., J. D. Congdon, K. T. Scribner, and J. D. Capps. 2011. Variation in female reproductive quality and reproductive success of male Midland Painted Turtles (*Chrysemys picta marginata*). *Canadian Journal of Zoology* 89:1136–1145.
- Miaud, C., R. Guyétant, and H. Faber. 2000. Age, size, and growth of the alpine newt, *Triturus alpestris* (Urodela: Salamandridae), at high altitude and a review of life-history trait variation throughout its range. *Herpetologica* 56:135–144.
- Mitchell, T. S., J. M. Refsnider, A. Sethuraman, D. A. Warner, and F. J. Janzen. 2017. Experimental assessment of winter conditions on turtle nesting behavior. *Evolutionary Ecology Research* 18:271–280.
- Moran, E. V., F. Hartig, and D. M. Bell. 2016. Intraspecific trait variation across scales: implications for understanding global change responses. *Global Change Biology* 22:137–150.
- Parker, G. A., and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *The American Naturalist* 128:573–592.
- Poulin, R. 1995. Clutch size and egg size in free-living and parasitic copepods: a comparative analysis. *Evolution* 49:325–336.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Raffard, A., A. Lecerf, J. Cote, M. Buoro, R. Lassus, and J. Cucherousset. 2017. The functional syndrome: linking individual trait variability to ecosystem functioning. *Proceedings of the Royal Society B* 284:20171893.
- Rollinson, N., and R. J. Brooks. 2007. Proximate constraints on reproductive output in a northern population of Painted Turtles: an empirical test of the bet-hedging paradigm. *Canadian Journal of Zoology* 85:177–184.
- Rollinson, N., and R. J. Brooks. 2008. Sources and significance of among-individual reproductive variation in a northern population of Painted Turtles (*Chrysemys picta*). *Copeia* 2008:533–541.
- Ryan, K. M., and P. V. Lindeman. 2007. Reproductive allometry in the common map turtle, *Graptemys geographica*. *The American Midland Naturalist* 158:49–59.
- Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* 17:667–693.
- Schwarz, W., and S. Meiri. 2017. The fast-slow life-history continuum in insular lizards: a comparison between species with invariant and variable clutch sizes. *Journal of Biogeography* 44:2808–2815.
- Segers, F., and B. Taborsky. 2010. Egg size and food abundance interactively affect juvenile growth and behaviour. *Functional Ecology* 25:166–176.

- Shine, R., and R. A. Seigel.** 1996. A neglected life-history trait: clutch-size variance in snakes. *Journal of Zoology* 239:209–223.
- Smith, C. C., and S. D. Fretwell.** 1974. The optimal balance between size and number of offspring. *The American Naturalist* 108:499–506.
- van Dijk, P. P.** 2011. *Clemmys guttata* (errata version published in 2016). The IUCN Red List of Threatened Species 2011:e.T4968A97411228.
- Vitt, L. J.** 1977. Observations on clutch and egg size and evidence for multiple clutches in some lizards of southwestern United States. *Herpetologica* 33:333–338.
- Wilkinson, L. R., and J. W. Gibbons.** 2005. Patterns of reproductive allocation: clutch and egg size variation in three freshwater turtles. *Copeia* 2005:868–879.
- Williamson, L., V. Garcia, and J. R. Walters.** 2016. Life history trait differences in isolated populations of the endangered Red-cockaded Woodpecker. *Ornis Hungarica* 24:55–68.
- Wilson, D. S.** 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology* 76:1884–1892.
- Wilson, D. S., H. R. Mushinsky, and E. D. McCoy.** 1999. Nesting behavior of the Striped Mud Turtle, *Kinosternon baurii* (Testudines: Kinosternidae). *Copeia* 1999:958–968.