Volume 32 (July 2022), 130-141

Herpetological Journal FULL PAPER

https://doi.org/10.33256/32.3.130141

Published by the British Herpetological Society

Temporal partitioning of hatching, maturation, and surface activity by reptiles in Florida longleaf pine-wiregrass sandhills

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Temporal partitioning of life history traits among syntopic reptiles can facilitate co-occurrence, but may be influenced by environmental factors and evolutionary history. We used 24 years of continuous capture data in the Florida sandhills to evaluate the timing and duration of hatching, maturation and/or surface activity for ten reptile species, spanning multiple clutch strategies, taxonomic relationships, and habits. We hypothesised: i) species would differ in seasonal timing of hatching and maturation; ii) hatching and maturation periods would be more seasonally-synchronised in fossorial than terrestrial or semi-aquatic reptiles; iii) monthly and annual temperature anomalies would be positively related to hatching, maturation, and surface activity anomalies, and iv) groupings of reptiles by clutch strategy, taxonomic relationship, and habit, would explain more variation in the timing and duration of hatching and maturation than species alone. Seasonal timing of response variables varied widely among species. Hatching peaked for > 1 species during most calendar months. Maturation and surface activity periods ranged from aseasonal to highly-seasonal among species. Hatching began 1.5 months earlier and was more prolonged for terrestrial than fossorial species overall. Hatching peaked in early to mid-summer for terrestrial and fossorial species, and winter for the semi-aquatic *Kinosternon subrubrum*. Terrestrial and fossorial species did not differ in average timing, duration, or overlap of maturation periods; semi-aquatic *Liodytes pygaea* matured more consistently across all seasons than other species. Monthly temperature anomalies were negatively correlated with monthly maturation for *Plestiodon egregius*. Annual temperature and precipitation anomalies were related to annual hatching, maturation, and surface activity trends for several species. Taxonomic relationship, habit, and species explained some variation in hatching and maturation timing and duration. Our results illustrate the influence of environment and evolutionary relationships on the timing of important life history traits.

Keywords: Age class, Drift fence, Community, Interspecific, Life history

INTRODUCTION

Niche partitioning and life history traits are major factors regulating species coexistence.Several studies demonstrate how syntopic reptile species partition microhabitats for thermoregulation (Tadevosyan, 2007; Buckley & Jetz, 2010), and food (Schoener, 1968; Pianka, 1973; Lelièvre et al., 2012), but temporal partitioning of hatching and maturation has received little attention (Post, 2019). Information on ontogenetic life history traits and their variation across syntopic reptile species is needed to better understand how they coexist. For example, taxonomic relationships related to physiology and ecological habit (fossorial, terrestrial, or semi-aquatic) may influence temporal partitioning of hatching and maturation by affecting thermal preferences (Brattstrom, 1965; Clusella-Trulas & Lee, 2014), and dependence on warm temperatures to accelerate embryonic development and juvenile growth rates (Sinervo & Adolph, 1989; Van Damme et al., 1992; Georges et al., 2005).

Habit modifies exposure to environmental conditions (e.g. temperature) and may, in turn, influence the timing of life history traits. For example, subterranean temperature is relatively constant year-round compared to surface temperature (Burda et al., 2007; Pike & Mitchell, 2013), potentially allowing for greater seasonal synchronisation of hatching and maturation by fossorial than terrestrial reptile species. In addition, species inhabiting subtropical regions (e.g. central Florida) may vary more widely in their timing of hatching, maturation, and surface activity than those limited by cold winter temperatures in temperate regions. Conversely, the paucity of cold weather adaptations found in many subtropical reptiles (Clusella-Trulas & Lee, 2014) may increase the sensitivity of hatching, maturation, or surface activity periods to monthly or annual temperature anomalies.

We used 24 years of continuous trapping data from longleaf pine-wiregrass sandhills to examine the temporal partitioning of hatching, maturation and surface activity among 10 reptile species within three categories representing fossorial, terrestrial and semi-aquatic habits. Florida sandhills are an ideal ecosystem to assess patterns of temporal partitioning among reptiles bound by similar ecological conditions, as reptile diversity is high (Dodd, 1992; Greenberg et al., 1994; Pearlstine et al., 2002; Means et al., 2004), and a warm climate offers a long 'season'

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for potential hatching, maturation, and surface activity (Myers, 1990; Button et al., 2019). We hypothesised:

i) reptile species would differ in their seasonal timing of hatching, maturation, and surface activity;
ii) hatching and maturation periods would be more seasonally synchronised in fossorial than terrestrial or semi-aquatic reptiles;
iii) monthly and annual temperature anomalies would be positively correlated with monthly anomalies in reptile hatching, maturation, and surface activity, and
iv) clutch strategy, taxonomic relationship, and habit would provide more information about hatching and maturation periods than species alone.

METHODS

Study area

We captured reptiles adjacent to eight small (0.10–0.37 ha), ephemeral, groundwater-driven sinkhole ponds, embedded within xeric longleaf pine *Pinus palustris* and wiregrass *Aristida sp*. uplands of the Floridan Aquifer System region, in Ocala National Forest, Marion County, Florida (Greenberg et al., 2015). Six ponds were located within ~0.7 km of one another; two were ~9.5 km south of the others (Fig. S1). Average monthly temperatures (February 1997–December 2017) ranged from 13.5 ˚C in January to 28.6 ˚C in August (Fig. S2). Average annual precipitation (1995–2017) was 140.7 cm, with more than half occurring during late spring and summer. Wetland depths were generally highest in winter and lowest in summer because of rainfall patterns, groundwater recharge (Greenberg et al., 2015; 2017), and low evapotranspiration in winter (Knowles et al., 2002). The upland forest matrix surrounding the study ponds consisted mostly of savanna-like sandhills with wiregrass-forb ground cover and widely-spaced longleaf pine trees with patches of hardwood trees and sand pine *Pinus clausa*. Common soils were well-to-excessively drained Entisols with < 5 % silt plus clay in the upper profile, classified in the hyperthermic, uncoated families of Spodic (Paola series) and Typic (Astatula series) Quartzipsamments (Aydelott et al., 1975). Study pond elevations ranged from 4–26 m.

Field methods

We installed 7.6 m-long drift fences spaced 7.6 m apart around the perimeter of each pond such that 50 % of each pond was fenced. We installed pitfall traps (19-litre buckets) on the inside and outside of each fence at both ends (four per fence), and positioned a double- or single-ended funnel trap (one each per fence) at its midpoint on opposite sides. We embedded a PVC pipe (5-cm diameter; ~1.4 m height) at one end of each fence to attract anoles. We placed a sponge in each pitfall trap and moistened as needed during trap checks to reduce the likelihood of animal desiccation. We checked traps three times weekly from 1 February 1994–31 December 2017, or sometimes less frequently (one to two times weekly) during cold months (November–early March), when capture rates were low. We identified, measured snout-vent length (SVL), and marked all captured individuals using toe- (lizards) or scale-clipping (snakes), or scute-notching (turtles). We used a max-min thermometer to measure maximum and minimum air temperature weekly, and used a rain gauge to measure precipitation approximately three times weekly (February 1997–December 2017).

Study species and categories

We focused our analyses on ten commonly captured species representing three ecological habit categories: terrestrial (Southeastern five-lined skink *Plestiodonin expectatus*, six-lined racerunner *Aspidoscelis sexlineata,* green anole *Anolis carolinensis*, Florida scrub lizard *Sceloporus woodi*, Eastern garter snake *Thamnophis sirtalis*); fossorial (mole skink *P. egregius*, little brown skink *Scincella lateralis,* Florida crowned snake *Tantilla relicta*); and semi-aquatic (Eastern mud turtle *Kinosternum subrubrum*, black swamp snake *Lyodytes pygaea*). These species spanned five major clades, including Testudines (*K. subrubrum)*; Scincomorpha (*P. egregius*, *P. inexpectatus*, *S. lateralis)*; Laterata (*A. sexlineata)*; Iguanomorpha (*A. carolinensis*, *S. woodi)*; and Serpentes (*L. pygaea*, *T. relicta*, *T. sirtalis)*. Four species (*P. egregius, P. inexpectatus, L. pygaea, T. relicta*) are known to produce one clutch per year, while six (*K. subrubrum, S. lateralis, A. sexlineata, A. carolinensis, S. woodi, T. sirtalis*) can produce multiple clutches per year.

Adjustments for flooding

We used only first captures (i.e. no recaptures) in all data analyses. We divided each year into 12, month-long periods to assess seasonal timing of hatching and maturation for each species, pooling data from all ponds. Trap closures due to infrequent flooding necessitated adjustments to capture data during some months at some ponds. We considered a pond to be 'closed' during a given month if flooding reduced its number of monthly trap-nights by > 50 %. Data were adjusted by dividing total monthly first-captures (by age class and species) by the proportion of 'open' ponds. For example, if we captured 100 adults of a species in October 2008, but only five of eight ponds were 'open', the number of captures was adjusted to 160 (100/0.625). We also grouped capture data by year for annual-scale analyses of hatching, maturation, and surface activity, correcting for flood-related trap closures as described above. Flood-related closures that reduced monthly trap-nights at a pond by > 50 % were rare (mean ± SE = 9 % ± 2 %; range = 4–24 % of months) and occurred most often during September–December.

Age class delineation

We assigned individuals to a hatchling, intermediate juvenile, maturing juvenile, or adult age class based on SVL cutoffs derived from published literature (Palmer & Braswell, 1995; Conant & Collins, 1998) and professional judgement (Table 1). We defined 'hatchlings' as individuals with SVLs less than the sum of the minimum SVL plus 15 % of the range of SVLs recorded for all captures of the same species. For example, if SVLs of a given species ranged 10–110 mm (range = 100 mm), individuals < 25 mm (10 + 100*0.15) SVL were classified as 'hatchlings' (Table 1). 'Maturing juveniles' comprised individuals within +10 %

Table 1. Age-class size (snout-vent length) cutoffs and ecological groupings (clutch strategy, taxonomic relationship, and habit) used in analyses, and total (February 1994–December 2017) number of first-captured hatchling, intermediate juvenile, maturing juvenile, and adult age classes for 10 reptile study species, Ocala National Forest, Marion County, Florida[1]. S = single-clutch and M = multi-clutch.

				Hatchlings		Intermediate Juveniles		Maturing Juveniles		Adults		Total
Species[2]	**Clutch Strategy**	**Taxonomic Category**	**Habit[3]**	**Size (mm)**	**n**	**Size (mm)**	**n**	**Size (mm)**	**n**	**Size (mm)**	**n**	**n**
P. egregius	S	Scincomorpha	F	< 23.7	39	23.7–35.0	144	35.1–42.9	185	> 42.9	206	574
S. lateralis	M	Scincomorpha	F	< 18.1	90	18.1–25.1	305	25.2–30.8	346	> 30.8	1,596	2,337
T. relicta	S	Serpentes	F	< 64.8	8	64.8–108.8	99	108.9–133.1	443	> 133.1	529	1,079
Habit Subtotal			F		137		548		974		2,331	3,990
K. subrubrum	M	Testudines	SA	< 33.6	270	33.6–48.9	10	49.0–59.9	13	> 59.9	196	489
L. pygaea	S	Serpentes	SA	< 103.2	13	103.2–188.9	194	189.0–231.0	235	> 231	321	763
Habit Subtotal			SA		283		204		248		517	1,252
A. carolinensis	M	Iguanomorpha	T	< 24.7	18	24.7–32.3	158	32.4–39.6	327	> 39.6	912	1,415
A. sexlineata	M	Laterata	T	< 30.9	135	30.9⍰–45.8	1,152	45.9–56.1	1,134	> 56.1	1,334	3,755
P. inexpectatus	S	Scincomorpha	T	< 30.5	272	30.5–49.9	908	50.0–61.1	354	> 61.1	368	1,902
S. woodi	M	Iguanomorpha	T	< 27.1	13	27.1–37.2	48	37.3–45.4	114	> 45.4	104	279
T. sirtalis	M	Serpentes	T	< 191.9	82	191.9–259.9	78	260.0–317.6	58	> 317.6	92	310
Habit Subtotal			T		520		2,344		1,987		2,810	7,661
Total					940		3,096		3,209		5,658	12,903

[1] Due to low sample sizes we omitted *K. subrubrum* from maturation analyses, and omitted *A. carolinensis, L. pygaea, S. woodi*, and *T. relicta* from hatchling analyses; intermediate juveniles were omitted from both hatchling and maturation analyses.

[2] *P. egregrius = Plestiodon egregius* (mole skink), *S. lateralis = Scincella lateralis* (little brown skink), *T. relicta = Tantilla relicta* (Florida crowned snake), *K. subrubrum = Kinosternon subrubrum* (eastern mud turtle), *L. pygaea = Liodytes pygaea* (black swamp snake), *A. carolinensis = Anolis carolinensis* (green anole), *A. sexlineata = Aspidoscelis sexlineata* (six-lined racerunner), *P. inexpectatus = Plestiodonin expectatus* (southeastern five-lined skink), *S. woodi = Sceloporus woodi* (Florida scrub lizard), and *T. sirtalis = Thamnophis sirtalis* (common gartersnake).

[3] F = fossorial, SA = semi-aquatic, and T = terrestrial.

of an a priori juvenile-adult SVL cutoff. 'Adults' were all individuals larger than maturing juveniles. We defined 'intermediate juveniles' as individuals with SVLs falling above the upper size cutoff for hatchlings but below the lower size cutoff for maturing juveniles, defined above and in Table 1.

Data formatting

We calculated monthly anomalies in temperature and precipitation, and in hatching, maturation, and surface activity to assess their possible correlations. We treated first captures of all age classes except hatchlings (which often diverge in their responses to temperature/precipitation) as a proxy for surface activity. We calculated monthly anomalies of minimum, average, and maximum temperatures, or precipitation, by subtracting average monthly minimum, average, and maximum temperatures, or precipitation (n = 23 for January, n = 24 for all other months), from year-specific monthly temperatures or precipitation. For example, if the annual mean maximum July temperature was 40 ˚C and the maximum July 2010 temperature was 38 ˚C, the anomaly for maximum temperature in July 2010 was -2 ˚C. Similarly, we calculated monthly anomalies in the timing of hatching, maturation, or surface activity for each species by subtracting average monthly estimates of hatching, maturation, or surface activity from estimates within each specific month of the study.

Data analyses: timing of hatching

We used monthly hatchling captures to assess timing of hatching for each species (hypothesis i)) and habit category (fossorial and terrestrial; hypothesis ii)) within a given year. We assumed that a pulse of hatchling captures indicated recent hatching. We converted monthly hatchling captures to monthly proportions of total hatchling captures within a given year to standardise the scale (0–1) among years and species. For example, if we captured 20 of 50 total 2010 hatchlings during April, the proportion of April 2010 hatchling captures was 0.4. We averaged year-specific monthly proportions of hatchling captures (n = 23 for January; n = 24 for all other months) across all years to infer the timing of hatching. We recognise that two of our study species, *L. pygaea and T. sirtalis*, are viviparous and give birth to neonates but use the term 'hatchling' for simplicity.

Data analyses: timing of maturation

We used adult and maturing juvenile captures to estimate timing of maturation for each species (hypothesis i)) and habit (fossorial and terrestrial; hypothesis ii)); smaller age classes (hatchlings and intermediate juveniles) were omitted. We standardised capture data across all years and species by z-scoring (i.e. subtracting by the mean then dividing by the standard deviation) flooding-adjusted captures of age classes (adults and maturing juveniles) and species for each month, relative to the number of flooding-adjusted captures for other months within the same year. We treated z-scored adult captures as a proxy for a species' average monthly catchability, and subtracted z-scored adult captures from z-scored maturing juvenile captures to estimate the relative number of maturing juveniles in the population each month, compared to other months within the same year. For example, we interpreted high capture numbers (positive z-score) of maturing juveniles during a month of low catchability (negative z-score for adult captures) as an above-average number of maturing juveniles for that month relative to other months within the same year. We averaged relative monthly z-scores of maturing juveniles across all years (n = 23 for January and n = 24 for all other months) for each species to estimate seasonal timing of maturation.

Data analyses: environmental correlates of life history traits

We used generalised linear models (GLMs; Nelder & Wedderburn, 1972) to assess relationships of monthly temperature or precipitation anomalies with monthly hatching, maturation, or surface activity anomalies (hypothesis iii)). Minimum, average, and maximum temperature anomalies were highly correlated with one another, so we never included more than one in the same model. We constructed three GLM sets (hatching, maturation, and surface activity) for each species, each consisting of three initial, single predictor-based (minimum, average, or maximum temperature, or precipitation) GLMs, plus a null model. We used Akaike's Information Criterion (AICc) to rank models within each set (Akaike, 1998) and concluded null results if ΔAICc was < 3.0 for the null model relative to the highest-ranking model. Otherwise, we accepted the top-ranking model, and added season (winter, spring, summer, or autumn) as an interactive, second predictor variable if it improved the model's AICc score, to determine whether relationships of temperature or precipitation anomalies with hatching, maturation, or surface activity anomalies varied seasonally.

We also assessed environmental correlates of hatching, maturation, and surface activity across years. We calculated the median month of hatching and maturation for each species and year, then calculated these values relative to the average annual median hatching or maturation times across all study years. We repeated this procedure for the narrowest possible span of months within each year covering 95 % of all hatchling and maturing juvenile captures for each species. For example, if 95 % of hatchlings were captured over a span of 5 months (e.g. May–September) in 2015, compared to an average span of 4 months across all study years, the departure from normal for 'hatching period duration' was 5-4 = 1 month in 2015. For surface activity analyses, we subtracted the number of non-hatchling captures for each species within each year from the average annual number of non-hatchling captures across all years. For example, if we captured 100 non-hatchling *T. relicta* in an average year and captured 80 in 2015, then the departure of non-hatchling *T. relicta* captures in 2015 was -20. We used the same GLM and AICc procedures as above to compare models relating annual hatching, maturation, and surface activity to annual minimum, mean, and maximum temperatures, and precipitation. Years lacking temperature data for part of the year or lacking sufficient hatchling or maturing juvenile captures (i.e. n< 5 within a given year) were excluded from these analyses.

Data analyses: sensitivity of life history traits to clutch strategy, taxonomic relationship, and habit

We categorised each species within each of three groupings including clutch strategy (categories: single- or multi-clutch annually), taxonomic relationship (categories: Testudines, Iguanomorpha, Scincomorpha, Laterata, or Serpentes), and habit (categories: terrestrial or fossorial) to explore the relative importance of grouping method in explaining annual hatching and maturation patterns compared to species alone (hypothesis iv)). We calculated the standard deviation (sd) of average annual hatching or maturation parameters across categories within each grouping for both median hatching/maturation time and the duration of hatching/maturation (described previously). For example, if the collective median hatching time (month) was 5 (May) for the fossorial habit category, and 7 (July) for the terrestrial category, sd of the vector (5, 7) and the relative importance of habit for predicting median hatching time (i.e. sensitivity of median hatching time to habit) would be 1.4. If sd of this vector was 2.4 for the taxonomic relationship grouping, we considered median hatching time to be more sensitive to taxonomic relationship than habit (2.4 > 1.4).

RESULTS

We captured 12,903 total individuals of our ten study species over the 24-year study period, including 940 hatchlings, 3,096 intermediate juveniles, 3,209 maturing juveniles, and 5,658 adults (Table 1, Fig. 1). Hatchlings accounted for < 5 % of total captures for *A. carolinensis, L. pygaea, S. woodi,* and *T. relicta*, and maturing juveniles accounted for < 3 % of total captures for *K. subrubrum* (Table 1); this prevented analysis of hatching or maturation time, respectively, for these species.

Total detection frequency (all years and age classes combined for each species) exceeded its overall mean during early or mid spring (March or April), early or mid autumn (September or October) for *A. sexlineata, L. pygaea, P. inexpectatus, S. lateralis*, and *T. sirtalis*; mid–late spring (May) for *A. carolinensis*, and early spring–early summer (June) for *S. woodi*. The remaining three species had bimodal detection frequencies, with above-average

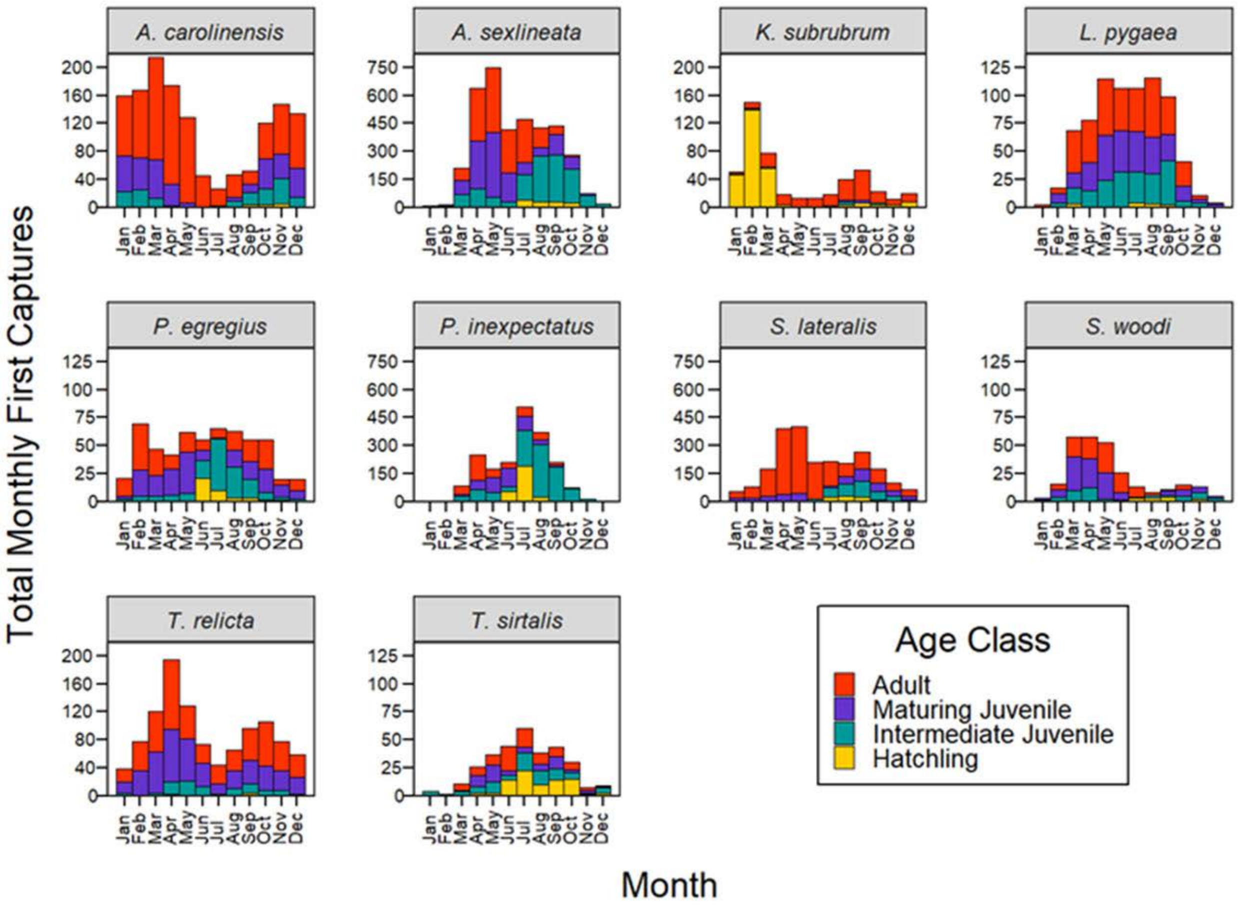

Figure 1. Total monthly number of first captured individuals (1994–2017 combined) by age class (see Table 1) for 10 reptile species, Ocala National Forest, Marion County, Florida. Note, first capture scales are not constant.

detections occurring throughout winter (December–February) and early autumn for *K. subrubrum*; late winter (February) and late spring–mid autumn for *P. egregius*, and; spring (March–May) and early–mid autumn for *T. relicta* (Fig. 1). Captures declined sharply in winter for most species but occurred with moderate frequency almost year-round for *A. carolinensis, P. egregius*, and *T. relicta*.

Interspecific variation in hatching and maturation

Average seasonal timing of hatching and maturation varied widely among species (n = 10; Figs. 2 & 3). Hatching periods spanned several months and overlapped among most species, but peaked in different months for different species, with peaks occurring for at least one species during all months except April, November, and December (Fig. 2). Hatching peaked in mid summer–mid autumn for *A. sexlineata, S. lateralis*, and *T. sirtalis*; late spring–mid summer for *P. egregius and P. inexpectatus*, and throughout winter and early spring for *K. subrubrum*. *Thamnophis sirtalis* hatching exhibited multiple small seasonal peaks during both mid summer and mid autumn (Fig. 2). The duration of seasonal peaks for hatching ranged from approximately 1–2 months for *P. egregius* and *P. inexpectatus*, to 5–6 months for *A. sexlineata* and *T. sirtalis*. Timing of maturation peaked in early–mid autumn for *A. carolinensis, A. sexlineata*, and *S. lateralis*; early summer for *P. inexpectatus*; late autumn–early spring for *S. woodi*, and biannually in late spring and early or late autumn for *P. egregius* and *T. sirtalis* (Fig. 3). Maturation was aseasonal (i.e. sd < 0.3 for average z-scored maturation values across the 12 months) for *T. relicta* and *L. pygaea*; weakly seasonal (sd = 0.3–0.4) for *P. egregius, S. woodi*, and *T. sirtalis*; moderately seasonal (sd = 0.4–0.6) for *A. carolinensis* and *A. sexlineata*, and; highly seasonal (sd > 0.6) for *P. inexpectatus* and *S. lateralis* (Fig. 3).

Influence of habit on hatching and maturation timing

Timing of hatching within a given year varied in relation to habit (n = 3) in multiple ways. For the terrestrial habit category (*A. sexlineata, P. inexpectatus*, and *T. sirtalis*), hatching exceeded 5 % of its annual total and began to sharply increase by mid March – nearly 1.5 months earlier than for the fossorial habit category (*P. egregius* and *S. lateralis*) (Fig. 4). The hatching period (middle 95 % of estimated hatching) was also 1.2 months longer for the terrestrial (7.7 months) than the fossorial (6.5 months) habit category. Fossorial and terrestrial habit categories both reached peak category-wide hatching in early–mid summer, whereas the only semi-aquatic species in our hatching analyses (*K. subrubrum*) hatched almost exclusively during winter (Fig. 2). Nonetheless, species was a better predictor of annual hatching times than terrestrial or fossorial habit categories.

In contrast to hatching periods, the average timing, overlap, and duration of maturation periods were similar in the terrestrial and fossorial habit categories (Fig. S3).

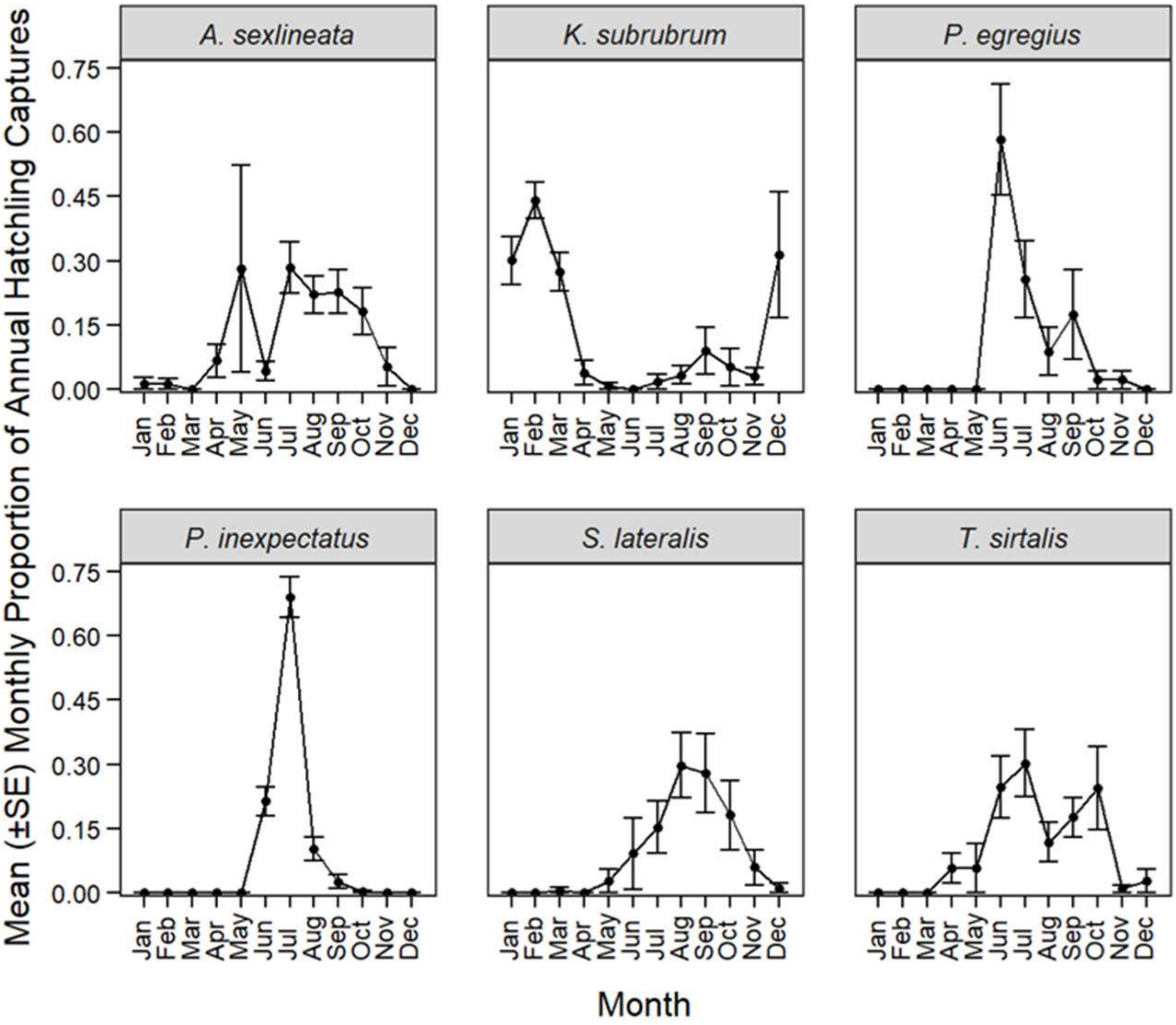

Figure 2. Mean (black points) (+SE; error bars) monthly proportions of annual hatchling captures (n = 23 years for January; 24 years for all other months) for six reptile species; Ocala National Forest, Marion County, Florida. Terrestrial species included *A. sexlineata, P. inexpectatus*, and *T. sirtalis*; fossorial species included *P. egregius* and *S. lateralis*; semi-aquatic species included only *K. subrubrum*. Proportions of hatchlings were calculated by dividing hatchling first captures (defined in Table 1) by total first captures.

Liodytes pygaea (the only semi-aquatic species included in our maturation analyses) maturation occurred more consistently across all seasons than fossorial or terrestrial habit categories (Fig. 3).

Influence of temperature anomalies on hatching, maturation, and surface activity

Monthly maturation anomaly (i.e. difference in monthly maturation compared to average for a given month) was negatively correlated with monthly average temperature anomaly for *P. egregius* (n = 240 months, P = 0.00623; AICc = 620.29; Fig. 5), though the effect size was modest (r = -0.197; 95 % CI = (-0.257, -0.043)) and interactions between temperature anomaly and season did not improve models for predicting maturation anomaly (ΔAICc = 6.16). Monthly temperature or precipitation anomalies did not influence monthly hatching, maturation, or surface activity anomalies for any other (n = 9) study species (i.e. ΔAICc< 3.0 for the null model; Table 2).

Annual temperature or precipitation anomalies were related to annual hatching, maturation, or non-hatchling surface activity patterns for several tested species (all age classes were not analysed for all species due to insufficient sample sizes). Model comparisons (i.e. >3 AICc units better [lower] than a null model) suggested that high annual mean temperature (i.e. positive annual temperature anomaly) was associated with delayed *S. lateralis* hatching, high weekly minimum temperatures across the year were associated with delayed *P. inexpectatus* maturation, and high weekly maximum temperatures across the year were associated with reduced *K. subrubrum* surface activity. In addition, high annual precipitation was associated with delayed birth of *T. sirtalis* neonates and reduced surface activity by *A. sexlineata*, (Table 2; Figs. 6 & 7). We found no evidence that annual temperature or precipitation anomalies influenced annual maturation, hatching, or surface activity anomalies (differences in these variables relative to average) for other study species.

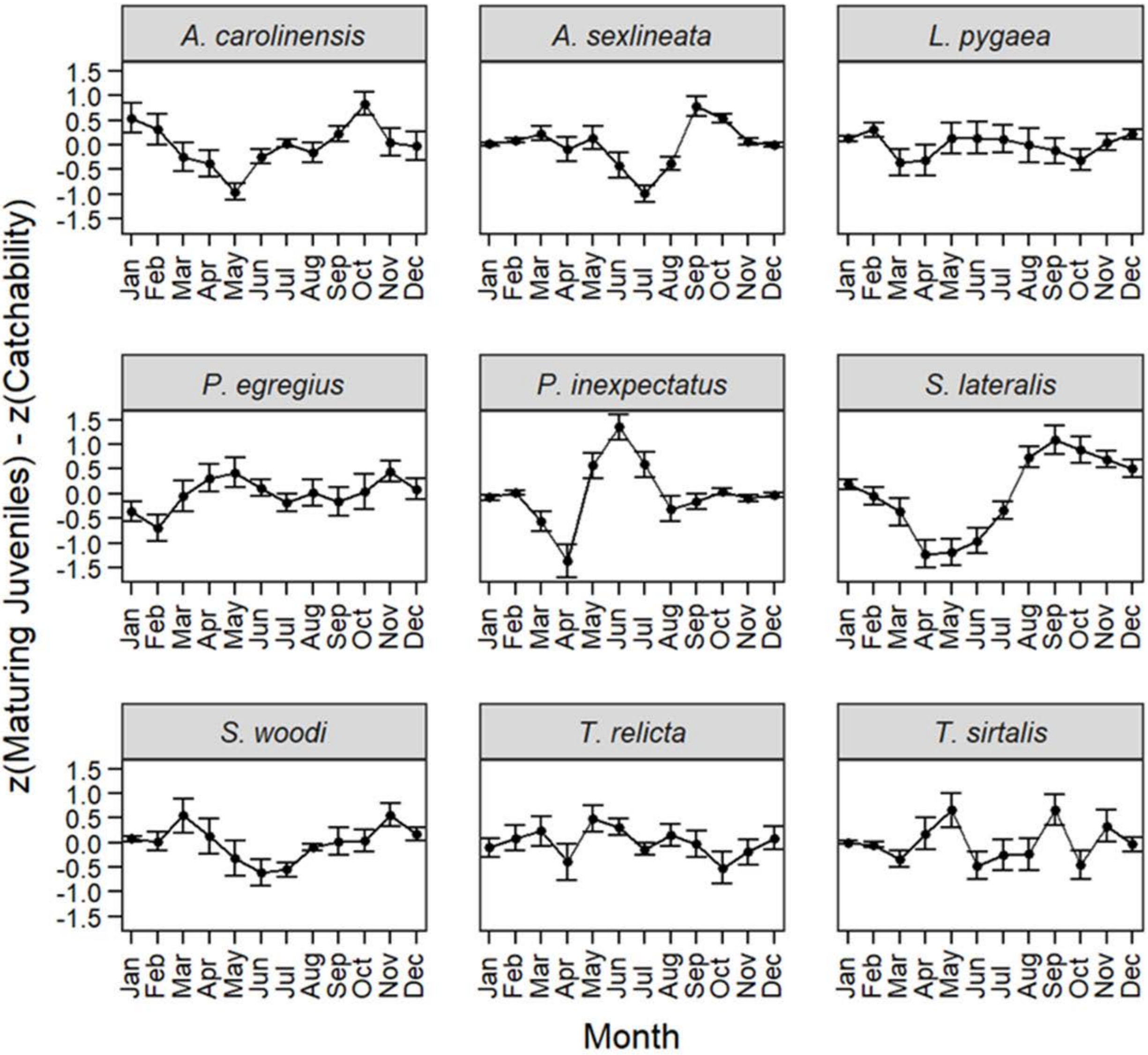

Figure 3. Estimated, standardized mean (black points) (+SE; error bars) monthly (n = 23 years for January; 24 years for all other months) maturation z-scores, for reptile species used in maturation analyses; Ocala National Forest, Marion County, Florida.

Influences of clutch strategy, taxonomic relationship, and habit on species' hatching and maturation patterns

Average hatching and maturation parameters (median timing and duration) varied widely in their sensitivity to clutch strategy, taxonomic relationship, and habit groupings relative to species alone (Fig. S4). Median hatching time and hatching period duration were both more sensitive to species than any of other grouping, but species, taxonomic relationship and/or habit were all similar in their relative influence on median maturation time and maturation period duration. All hatching and maturation parameters were relatively insensitive to clutch strategy.

DISCUSSION

Our results showed wide variation in the timing, duration, and seasonal peaks of hatching and maturation periods among study species (hypothesis i)), and generally supported our hypothesis ii): that habit (e.g. terrestrial or fossorial) may be an important influence on these life history traits. The longer hatching period seen in the terrestrial than fossorial habit category could ensure that at least some hatchlings survive by avoiding stochastic, unfavourable short-term conditions (e.g. unusually cold weather) that are more frequent in terrestrial than fossorial environments (Burda et al., 2007; Pike & Mitchell, 2013). Winter hatching by semi-aquatic *K. subrubrum*, and consistent year-round maturation by semi-aquatic *L. pygaea* also suggested that cold air temperatures are less limiting on hatching and maturation for the semi-aquatic than the fossorial or terrestrial habit categories. In addition, overall higher water levels in winter (Greenberg et al., 2015) increase the likelihood of aquatic habitat availability. Maturation periods were similar between fossorial and terrestrial habit categories, indicating that a relatively constant year-round subterranean temperature in the sandy soils of our study area (Burda et al., 2007; Pike & Mitchell, 2013) was not an important driver of maturation period for the fossorial species group.

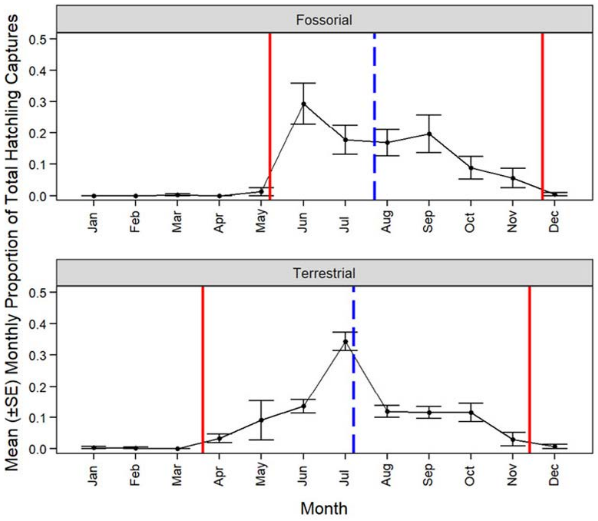

Figure 4. Mean (black points) (+SE; error bars) monthly proportion (n = 23 years for January; 24 years for all other months) of total hatchling captures of fossorial (*P. egregius* and *S. lateralis*) and terrestrial (*A. sexlineata, P. inexpectatus*, and *T. sirtalis*) reptile habit categories, Ocala National Forest, Marion County, Florida. Dashed blue lines reflect peak (i.e., mean) hatching time; solid red lines represent cutoffs used to determine an approximate 'start' and 'end' of the hatching period, based on 95 % of estimated hatching falling between these cutoffs.

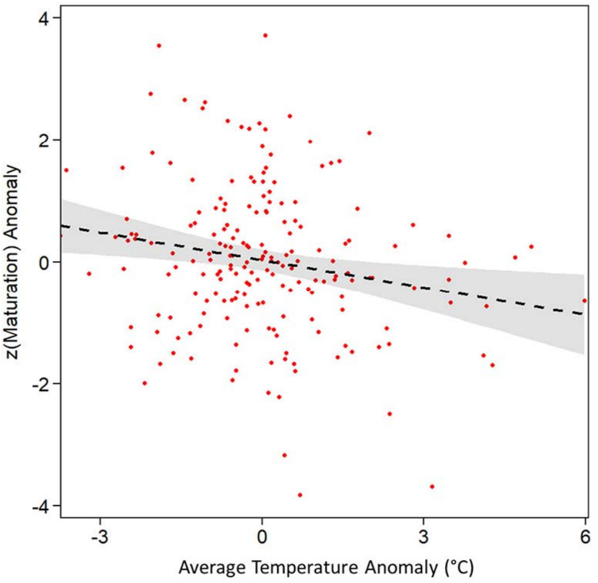

Figure 5. The relationship between average monthly temperature anomaly and z-scored maturation for P. egregious, Ocala National Forest, Marion County, Florida. The black line and gray shading represent the fitted model (r =-0.197) and its 95% confidence interval, respectively. Red points represent monthly temperature anomaly and maturation anomaly data used to model the fitted relationship (i.e., observed values).

Therefore, our hypothesis that hatching and maturation periods would be more seasonally-synchronised in the fossorial than terrestrial or semi-aquatic species groups received mixed support overall. As the climate warms, habit may therefore attenuate changes in hatching periods more for fossorial than terrestrial reptiles, but is less likely to attenuate changes in the timing or duration of maturation.

Monthly anomalies of minimum, average, or maximum temperatures or precipitation compared to normal had no detectable effect on the monthly timing of hatching, maturation, or surface activity for most study species, suggesting that seasonal timing of these life history traits is either relatively inelastic or not vulnerable to temperature deviations within the ranges tested. This did not support our original hypothesis of a positive relationship between temperature anomaly and hatching or maturation anomaly (hypothesis iii)) and was surprising, since warm temperatures are known to accelerate the embryonic development and/or juvenile growth of many reptile species (Sinervo & Adolph, 1989; Van Damme et al., 1992; Georges et al., 2005). Our study species may not be able to capitalise on abnormal short-term (monthly) weather patterns that would benefit their survival during life history transitions or surface activity under climate change. Instead, our study species' patterns of hatching, maturation, and surface activity appeared relatively inflexible over monthly timespans, and were only (for some species) modified when abnormal temperatures or precipitation persisted over much longer (e.g. annual; see below) periods. *Plestiodon egregius* was an exception; z-scored monthly maturation anomaly increased for this species during months of unusually cool weather, suggesting that moderately cool soil temperatures accelerated its maturation. Mount (1963) also suggested that *P. egregius* prefer cooler temperatures, noting they were active near the ground surface of pocket gopher mounds most often during "cooler months of the year."

Although monthly hatching, maturation, and surface activity trends appeared unrelated to monthly temperature and precipitation anomalies for most species, multiple species varied in their annual hatching, maturation, and surface activity trends across annual temperature and precipitation departure gradients (Figs. 6 & 7). Thus, our hypothesis iii) was supported across annual, but not monthly timescales. For example, non-hatchling *K. subrubrum* reduced their surface activity during hot years, which may have indicated a reduced ability to disperse in search of suitable aquatic habitats. In addition, higher than normal annual temperatures were associated with delayed *S. lateralis* hatching and *P. inexpectatus* maturation; future studies of these species' thermal optima during embryonic and juvenile development are thus warranted. Annual temperatures in our study region are projected to increase by 2–4 ˚C by 2071–2099 under climate change (Melillo et al., 2014), which may impact *K. subrubrum, S. lateralis*, and *P. inexpectatus*. For example, *K. subrubrum* populations may become more fragmented if increasing temperatures limit future dispersal between wetlands. In addition, delayed hatching in *S. lateralis* and delayed maturation in *P. inexpectatus* under climate change may lead to overall smaller body sizes in young-of-year individuals during winter, and thus fewer prey options due to smaller gape size during a period of the year when foraging opportunities are already limited. However, *S.*

Table 2. AICc tables for GLMs relating annual species maturation, hatchling, or non-hatchling surface activity to annual temperature and precipitation trends, Ocala National Forest, Marion County, Florida. Only models where the top-ranking model was at least three AICc units lower than the null model are shown. K = number of model parameters; AICc = AICc score of model; ΔAICc = difference in AICc score between a given model and the top-ranking model; ModelLik = model likelihood; AICcWt = AICc-based model weight. See Table 1 footnotes for species codes.

Analysis	Model	K	AICc	ΔAICc	ModelLik	AICcWt
P. inexpectatus Annual Maturation	Median Maturation Time ~ Minimum Temperature	3	35.78	0.00	1.00	0.73
	Median Maturation Time ~ Average Temperature	3	39.25	3.46	0.18	0.13
	Median Maturation Time ~ 1 (Null Model)	2	40.04	4.25	0.12	0.09
	Median Maturation Time ~ Annual Precipitation	3	42.24	6.46	0.04	0.03
	Median Maturation Time ~ Maximum Temperature	3	42.56	6.78	0.03	0.02
A. carolinensis Annual Hatching	Median Hatching Time ~ Annual Precipitation	3	39.60	0.00	1.00	0.85
	Median Hatching Time ~ 1 (Null Model)	2	43.51	3.91	0.14	0.12
	Median Hatching Time ~ Minimum Temperature	3	47.48	7.88	0.02	0.02
	Median Hatching Time ~ Average Temperature	3	48.83	9.23	0.01	0.01
	Median Hatching Time ~ Maximum Temperature	3	49.11	9.51	0.01	0.01
S. lateralis Annual Hatching	Median Hatching Time ~ Average Temperature	3	35.59	0.00	1.00	0.73
	Median Hatching Time ~ Minimum Temperature	3	39.05	3.46	0.18	0.13
	Median Hatching Time ~ 1 (Null Model)	2	39.51	3.93	0.14	0.10
	Median Hatching Time ~ Annual Precipitation	3	42.44	6.85	0.03	0.02
	Median Hatching Time ~ Maximum Temperature	3	43.41	7.83	0.02	0.01
T. sirtalis Annual Hatching[1]	Median Hatching Time ~ Annual Precipitation	3	57.49	0.00	1.00	0.80
	Median Hatching Time ~ 1 (Null Model)	2	61.64	4.15	0.13	0.10
	Median Hatching Time ~ Minimum Temperature	3	62.81	5.32	0.07	0.06
	Median Hatching Time ~ Average Temperature	3	64.46	6.97	0.03	0.02
	Median Hatching Time ~ Maximum Temperature	3	64.65	7.16	0.03	0.02
A. sexlineata Annual Surface Activity	Total Non-hatchling Captures ~ Annual Precipitation	3	227.25	0.00	1.00	0.93
	Total Non-hatchling Captures ~ 1 (Null Model)	2	234.46	7.21	0.03	0.03
	Total Non-hatchling Captures ~ Average Temperature	3	234.50	7.25	0.03	0.02
	Total Non-hatchling Captures ~ Maximum Temperature	3	235.62	8.37	0.02	0.01
	Total Non-hatchling Captures ~ Minimum Temperature	3	236.86	9.61	0.01	0.01
K. subrubrum Annual Surface Activity	Total Non-hatchling Captures ~ Maximum Temperature	3	56.78	0.00	1.00	0.70
	Total Non-hatchling Captures ~ 1 (Null Model)	2	60.44	3.66	0.16	0.11
	Total Non-hatchling Captures ~ Average Temperature	3	60.66	3.88	0.14	0.10
	Total Non-hatchling Captures ~ Annual Precipitation	3	61.63	4.85	0.09	0.06
	Total Non-hatchling Captures ~ Minimum Temperature	3	63.01	6.23	0.04	0.03

[1] Our results for *A. carolinensis* should be treated with caution because no years of our study had simultaneously below-average precipitation and sufficient (>10) *A. carolinensis* hatchling captures to be included in this analysis.

lateralis foraging may be less affected by seasonal changes in resource availability than for *P. inexpectatus*, due to more stable abiotic conditions (e.g. soil temperature, which directly impacts body temperature and may indirectly impact foraging by affecting prey availability) experienced underground versus aboveground. In addition to temperature-related trends, non-hatchling *A. sexlineata* were less surface active during wet than dry years, consistent with the dependence of teiids on sunlight (precluding cloudy skies and rain) for thermoregulation (Sartorius et al., 1999). Higher than normal annual precipitation was also associated with delayed birth of *T. sirtalis* neonates, but potential reasons for this trend are less clear. Compared to temperature, current climate projections suggest modest (<10 %) changes in mean annual precipitation for Florida by 2071–2099 (Melillo et al., 2014), suggesting minor-to-moderate impacts on *A. sexlineata* and *T. sirtalis*. We found no support for annual weather-related hatching, maturation, or surface activity trends for any other species, possibly due to < 20 years

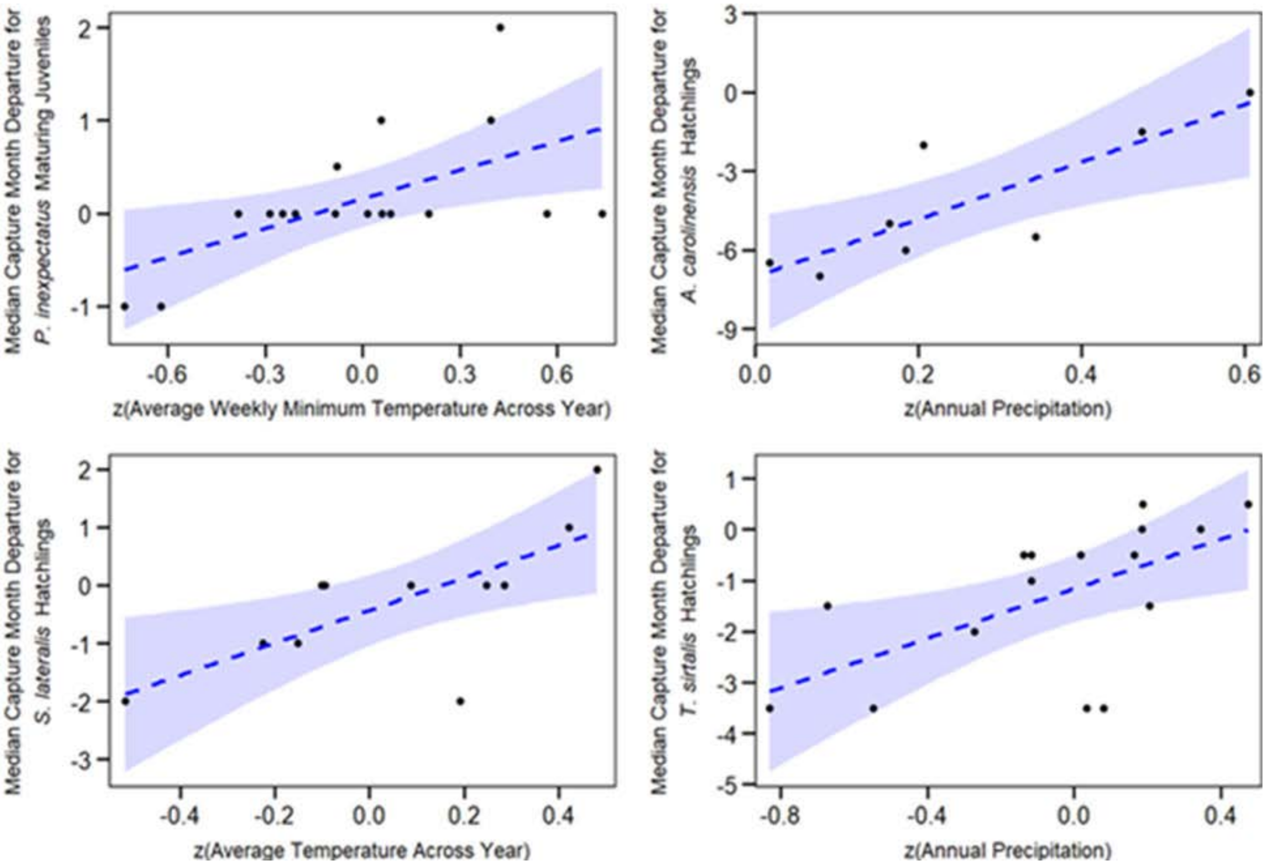

Figure 6. Generalised linear models showing potential effects of annual temperature and precipitation departures on changes in the timing of maturation and hatching, for selected species (Table 2), Ocala National Forest, Marion County, Florida. Negative or positive numbers for median hatchling captures represent years in which the median capture month of hatchlings occurred earlier or later in the year than average (1994–2017), respectively. Black points = observed data, dashed blue lines = fitted curves, and blue shading = 95 % confidence intervals.

of data (i.e. < 20 replicates) being usable in our annual analyses.

Infrequent captures of either hatchlings or maturing juveniles for five of our ten study species suggested that detectability varied widely among age classes for some species. Hatchlings comprised < 5 % of total *A. carolinensis, L. pygaea, S. woodi*, and *T. relicta* captures, suggesting they were less surface-active than other age classes. Lower detectability of hatchlings than other age classes has also been reported for *Gopherus polyphemus* (Gopher Tortoise) and *Pituophis melanoleucus mugitus* (Florida Pine Snake) in longleaf-wiregrass sandhills (Burger, 1998; Pike, 2006). Conversely, maturing juveniles comprised < 3 % of total *K. subrubrum* captures, suggesting that they reduced terrestrial activity during maturation. In our study, 94 % (n = 253/270) of *K. subrubrum* hatchlings were captured entering ponds, suggesting that they move into wetlands shortly after hatching and remain there until adulthood. Differential catchability among age classes has been documented in several other species (Lima & Moreira, 1993; Lind & Welsh, 1994; Wikelski & Trillmich, 1994), and presents a challenge for understanding the role that developmental phenology (e.g. timing of hatching and maturation) plays in shaping the temporal partitioning of species and habit-associated traits (e.g. foraging, courtship) during adulthood.

Our study addresses temporal partitioning of hatching and maturation among multiple sympatric reptiles, and relates species-specific hatching, maturation, and surface activity patterns to fluctuating temperatures and precipitation. Our results thus provide otherwise scarce information for several reptile species and an improved framework for future studies addressing causal mechanisms of temporal differences in these important life history traits. In addition, our findings highlight the potential for climate change to impact life history traits of Florida reptiles and illustrate the need for continued monitoring. Future research should consider how reptile hatching, maturation, and surface activity patterns may change given different emissions scenarios, and should clarify roles of thermal and moisture-related preferences as mechanisms underlying the patterns we observed among species and habit categories.

ACKNOWLEDGEMENTS

The findings and conclusions in this publication are those of the author(s) and should not be construed to represent any official USDA or US Government determination or policy. Funding was provided by the USDA Forest Service, Ocala National Forest; Longleaf Pine Ecosystem Restoration Program; Southern Research Station's

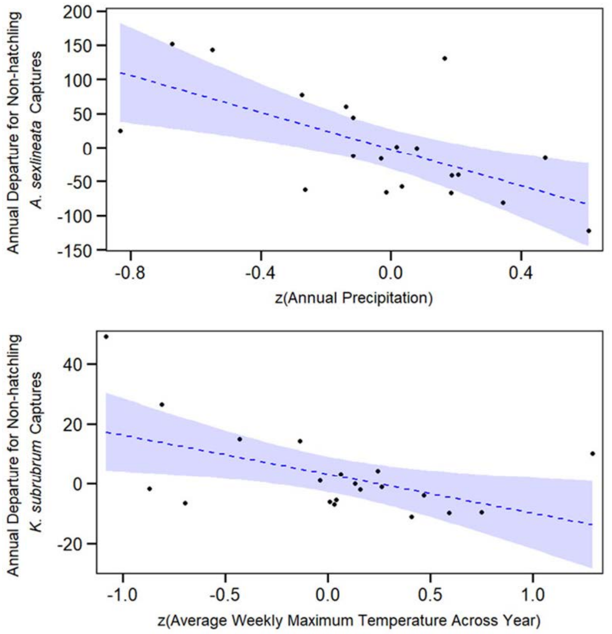

Figure 7. Generalized linear models showing potential effects of annual precipitation departures on changes on the total number of non-hatchlings captured, for selected species, Ocala National Forest, Marion County, Florida. For both of these species, model comparison revealed that the top-ranking models shown above had AICc scores > 3 units lower than the null model (Table 2). Departures in non-hatchling captures represent the number of new non-hatchling captures in a given year minus the average number of annual new non-hatchling captures across all years (1994–2017). Black points = observed data, dashed blue lines = fitted curves, and blue shading = 95% confidence intervals.

Intensive Management Practices Assessment (now defunct) and Upland Hardwood Ecology and Management research work units; Southern Region (R8); Department of Energy-Savannah River Operations (IA Agreement DE-AI09-76SR00056); and the Florida Fish and Wildlife Conservation Commission (contracts NG99-014 and C1195). We thank the many field assistants/site managers over the years, without whom this study would not have been possible: K. Garren, J. Weibe, S.A. Johnson, D.A. Johnson, J.S. Staiger, T. Sheltra (deceased), R.E. Ashton (deceased), D. Wooten, S. Wazny, M. Welker, C. Bugbee, S. Doucette-Riise, C.J. Kovach, R. Lara, L. Tirado, I. Luque-Montes, A. Heh, M. Bainum, C. Hartmann, G. Kamener, and R. Barker. J. Beach (deceased) volunteered full-time, 1994–2006. Many others helped as volunteers or short-term substitutes. We also thank University of Florida professors G.W. Tanner (retired) and A. Storfer, and Ocala National Forest staff L. Lowery (deceased), R. Lowery, C. Sekerak, J. Hinchee, and the fire crew for assistance. This research was approved by IACUC (permit No. 004-09WEC) and the Florida Fish and Wildlife Conservation Commission (permit No. LSSC-12-00021A).

Authors' contribution

Sky T. Button conducted all analyses, drafted the manuscript, and assisted with fieldwork during 2015–2016. Cathryn H. Greenberg procured funding, materials, and labour for the project, oversaw the project's operations, and edited the manuscript. James D. Austin helped procure funding and materials for the project, edited the manuscript, and helped provide local oversight of the project's operations.

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Accepted: 4 May 2022

Please note that the Supplementary Material for this article is available online via the Herpetological Journal website: https://thebhs.org/publications/the-herpetological-journal/volume-32-number-3-july-2022