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Drought affects sex ratio and growth of painted turtles in a long-term study in Nebraska

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ABSTRACT

Climate forecasts suggest the Great Plains of North America have increased risk of droughts during global warming. Environmental factors have potential to influence turtle populations in aquatic habitats through temperature-dependent sex determination and influences on food availability. Long-term studies are critical to evaluate the influence of climatic variation on turtles. We used a 12-year set of mark-recapture data collected from painted turtles (*Chrysemys picta*, $n = 162$) in a pond in Keith County, Nebraska during 2005–2016 to assess variation in sex ratio and growth dynamics. Southwest Nebraska experienced two periods of drought during our study (Palmer Hydrologic Drought Index [PHDI] range: -4.5 to 6.7). Despite a relatively stable depth of water in our study pond, the proportion of males in the second size class (carapace length 95–130 mm) decreased when the PHDI during their incubation period indicated hotter, drier conditions. Discrete, mean annual growth (G) of females >30 mm below asymptotic carapace length was greater during wetter years ($G_{non\text{-}drought} = 15.0$, $G_{drought} = 11.5$), and a drought coefficient (D) in our modified von Bertalanffy model reflected reduced growth of both males ($D = -0.0226$) and females ($D = -0.0393$) during drought years. Our long-term research provides context to the complexity by which turtle species may respond to changes in long-term climate conditions.

1. Introduction

Periods of drought have potential to impact wildlife populations through changes in food resources [1], impacts to habitat [2], changes in fire regime [3], and distribution of aquatic resources [4]. Climate forecasts for the next century suggest an increased risk of droughts during global warming for the tropics and mid-latitudes in both hemispheres [5], which heightens the need to understand drought dynamics and implications for species of conservation concern. Especially critical are long-term studies that shed light on drought effects in environmental systems [6].

Population viability analyses for species of turtles reveal that long-term droughts pose a critical risk [7], and ~75% of turtle species have a conservation status of "threatened" or more severe [8]. Environmental factors have a large impact on turtle populations by influencing reproduction, survival, and growth because of unique life history traits [9–11]. Many turtles experience temperature-dependent sex determination, which poses unique risks to changes in climate regime [12,13]. Growth of painted turtles is indeterminate [14], and growth rates can be used provide insights into the health of a population and the status of the environment and habitats supporting the species [15,16].

However, most studies on drought effects on pond turtles have been limited to a single drought cycle with period of study less than five years in length (e.g., [17–20]), with the exception of a 15-year study by Gibbons et al. [21]. Assessing patterns of growth under adequate levels of variation in climatic conditions can be difficult during a short-term study [15]. Studies that compare drought and non-drought conditions during short periods risk bias of definition, as it is difficult to establish the beginning and end of a drought [22].

Our goal was to use a 12-year, mark-recapture data set from a single pond to assess effects of drought on population structure, sex ratio, and growth of painted turtles (*C. picta*). Our objectives were to use the long-term data to (1) describe the size and sex structure of the population, (2), explore drought effects on sex ratios, and (3) evaluate effects of drought on annual growth and growth rates for repeated captures of individuals. Painted turtles are widespread across much of North America [23], and the species is not threatened with extinction [24]. We predicted that variation in soil temperatures and moisture would influence sex ratios in our sample and that the suite of environmental responses to drought would cause variation in growth rates through time.

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2. Material and methods

2.1. Study site

We focused this research on a 0.3-ha pond located near Ogallala, Nebraska in Keith County. The core region of the pond has a depth of 2–2.5 m. The pond is spring fed; thus, water level fluctuates by ~0.5 m with precipitation levels, and the pond's surface area is reduced by <10% during drought periods. The site is located in western high plains where the tallgrass and shortgrass prairies meet on the southern edge of the Sandhills region [25]. The North Platte River is ~5.6 km (3.5 mi) to the south of the pond, which is surrounded by rangeland used for cattle grazing. No fish have been documented in the pond during periodic seining, and northern crayfish (*Orconectes virilis*) and aquatic insects are abundant potential diet items. Annual estimated population size of painted turtles during our study ranged from 92 to 181 [26]. Snapping turtles (*Chelydra serpentina*) were the only other turtle species captured during our study.

2.2. Field methods

We captured painted turtles during 2005–2016 with the exception of 2009. Turtles were captured over periods of 2–55 days each year using basking traps and hoop nets [10,27]. We were aware that our trapping methods limited our ability to capture turtles with lengths less than ~70 mm [28], and methods were consistent across years. Turtles were removed from traps each morning (University of Nebraska-Lincoln IACUC Permits: 1074, 1568, 1993). We marked turtles with individual marks on marginal scutes [29], and in 2014 we began to use PIT markers as a secondary identification method. We recorded carapace length (mm), mass (g), and sex of each turtle before releasing to the pond [30].

2.3. Quantifying drought levels

We used mean Palmer Hydrologic Drought Index (PHDI; National Oceanic and Atmospheric Administration) data to quantify annual levels of drought during analyses. PHDI measures hydrological impacts of drought conditions to reflect groundwater conditions, reservoir levels, air temperature, and other values [31] relevant to aquatic turtles. We determined the mean PHDI in southwest Nebraska during the 12 months prior to June of each capture year [32] to quantify drought levels prior to capture and length measurements used to assess growth. For discrete analyses, we used negative PHDI values to indicate drought conditions and positive PHDI values for non-drought conditions. To assess drought effects on sex ratio we considered the six-year period prior to the year of capture to allow time for hatchlings to grow to lengths >95 mm to ensure our capture methods adequately sampled the size class. We obtained the mean PHDI in southwest Nebraska during years 3–6 prior to a given capture year [32] to match the years during which turtles in our second size class would have been hatched (e.g., we used PHDI data from 2004 to 2008 for the 2010 capture sample, 2005–2009 for 2011 sample, etc.). Our inferences regarding the relationship between drought conditions and sex ratio of our sample assumed drought conditions were accompanied by hotter temperatures, so we used a linear regression (PROC GLM, SAS Institute Inc., version 9.4) to confirm the relationship between drought conditions as reported by the PHDI during June of each year and the average temperature in the region during May and June.

2.4. Data analysis

2.4.1. Size structure and sex ratio

We created four size classes by quartiles of carapace length from the sample during the entire study (1st quartile: 68.0–95.0 mm, 2nd quartile: 95.1–130.0 mm, 3rd quartile: 130.1–165.0 mm, 4th quartile: 165.1–190.0 mm). We used the quartiles from our sample as an unbiased method to assess size classes, as we had no *a priori* information regarding the relationship between length of turtles at our study site and life history stages. However, we recorded presence of eggs in females during 2007 and 2008, and the reproductive size class for females roughly matched the 4th quartile of females > 165 mm.

We used our captured sample to estimate the male:female ratio of the second size class (95.1–130.0 mm) because it was the first size class that our traps adequately sampled. We used a general linear model (PROC GLM, SAS Institute Inc., version 9.4) to evaluate the effect of PHDI from the appropriate period on the proportion of males captured each year.

2.4.2. Mean annual growth

We used repeated measures of carapace length (mm) to determine growth across years for recaptured painted turtles. We ignored repeat captures within years, and we used the length measure from each individual's first capture in a given sampling year. Growth rates for painted turtles are sex-specific and asymptotic [16,33], so we only used turtles with carapace lengths that were at least 30 mm less than the sex-specific, asymptotic length for calculations of discrete annual growth. We used individuals of all lengths for growth rate analyses. For each 1-year capture interval, we calculated G, the discrete, mean annual change in carapace length for our sample. We only used individual's recapture events that were one year apart to estimate G. We performed two analyses for these data using discrete and continuous measures of drought level: (1) we compared sex-specific estimates of G for drought and non-drought years for the total sample, and (2) we used a linear regression to determine if sex-specific estimates of G were affected by the year-specific PHDI.

2.4.3. Growth rate

We used a modified von Bertalanffy model to estimate coefficients to describe nonlinear, indeterminant growth [15,34,35]. We used all repeated captures to estimate resulting individual length (L_R), growth rate (k) and asymptotic size (L_∞) given a starting length (L_C) and a gap in time between captures (t, years):

$$L_R = [L_\infty - L_C] \times \left[1 - e^{-(k-D)t}\right]$$

We modified the model to include a drought effect (D) as a modification to the growth rate (k), and we performed analyses separately for males and females [34]. We then used our growth model's estimates to create growth curves for male and female turtles to age 40. We set $L_C =$ 50 mm for two-year-old turtles, given the mean of visually aged samples from our study site. We used drought-specific coefficients (D) to create hypothetical growth curves for turtles living under constant drought or non-drought conditions.

We validated our growth model using individual turtles ($n = 19$) with multiple captures set aside from the initial regression analyses. For each pair of capture events ($n = 23$), we calculated the error in the prediction as the difference between the actual length at recapture and the predicted length.

3. Results

We documented 1067 captures of 369 unique individuals during the study (201 females, 168 males). We had 98 female turtles with recaptures across years (312 capture intervals) and 64 males with recaptures (194 capture intervals) during the study. Female carapace length ranged from 68 to 190 mm and male length ranged from 85 to 186 mm. Drought conditions were present at our study site in 2006, 2012, 2013, and 2014 (annual PHDI range: −4.5 to 6.7; mean = 1.2; Fig. 1). The average temperature during May and June of each of our study years was higher when drought conditions were more severe (negative PHDI values; $F_{1,11} = 10.99$, $P = 0.008$; slope = −0.392).

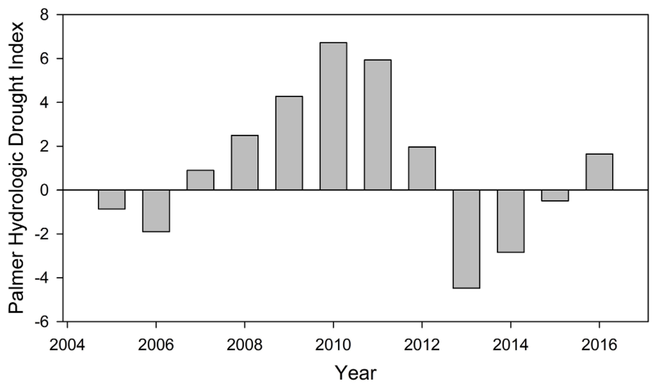

Fig. 1. Annual measures for the Palmer Hydrologic Drought Index in southwestern Nebraska during 2005–2016 for the period 12 months prior to June of year shown. Values of 0 are normal climatic conditions with negative values indicating drought conditions.

3.1. Size distribution and sex ratio

The size structure of our sample was weighted towards larger size classes for females compared to males (size class 1–4; mean across years, females: 0.07, 0.18, 0.36, 0.39; mean, males: 0.03, 0.46, 0.42, 0.09). The sex ratio of our multi-year sample was 0.39 (proportion males) and ranged from 0.26 (proportion males) to 0.51. The proportion of males in the second size class (across years: 0.59, range: 0.44–0.86) increased as the PHDI increased (P = 0.02, Fig. 2).

3.2. Mean annual growth

The mean annual growth (G) of females was greater during wetter years (slope = 0.87, SE = 0.28, $F_{1,7}$ = 9.43, P = <0.0001), but we found no effect of drought level on male annual growth ($F_{1,7}$ = 1.60, P = 0.25; Fig. 3). Average annual growth (G) for individuals >30 mm below asymptotic length was 12.9 mm (95% CI: ±1.0) for females and 4.0 (95% CI: ±0.4) for males. Annual growth (G) during non-drought years was less for males (mean $G_{non\text{-}drought}$ = 4.7 mm, 95% CI: ±1.0) than for females (mean $G_{non\text{-}drought}$ = 15.0, ±1.6), and drought lowered annual growth of females (mean $G_{drought}$ = 11.5, ±1.2) more than for males (mean $G_{drought}$ = 3.4, ±0.7).

The predicted asymptotic length (L_∞) for females was greater (L_∞=178.3 mm) than for males (L_∞ =166.9 mm) in our sample. Female turtles also had greater rates of growth (k) than males (male k = 0.1122, female k = 0.2269; Fig. 4, Table 1). During years classified as drought by the Palmer Hydrologic Drought Index, growth rates of both males and females had adjustments that led to smaller increments of growth (male D = −0.0226, female D = −0.0393; Fig. 4). The mean absolute error in model-predicted length in our validation exercise 1.7 mm (SD = 1.0) for males and 3.4 mm for females (SD = 3.4). As a proportion of the initial carapace length, the mean error in the predicted length was 0.01 (SD = 0.01) for males and 0.03 (SD = 0.03) for females.

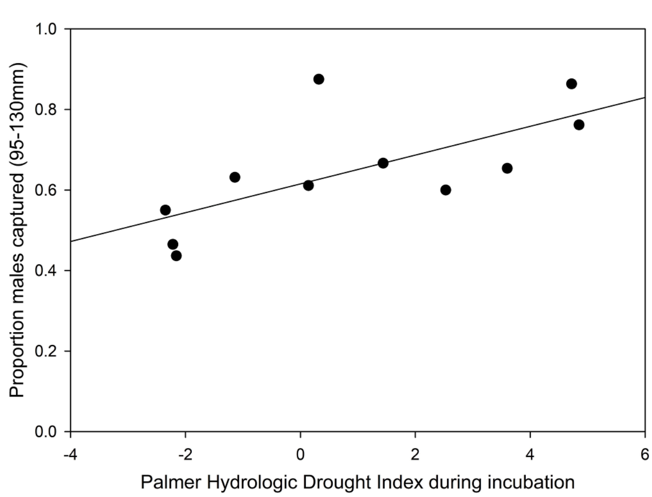

Fig. 2. The relationship between Palmer Hydrologic Drought Index (PHDI) in southwest Nebraska and the annual proportion of male painted turtles captured in size class two (95.1–130.0 mm) at a pond in Keith County, Nebraska during 2005–2016. PHDI values are from a four-year period beginning six years prior to the capture year of the sample used for the sex ratio; see text for details.

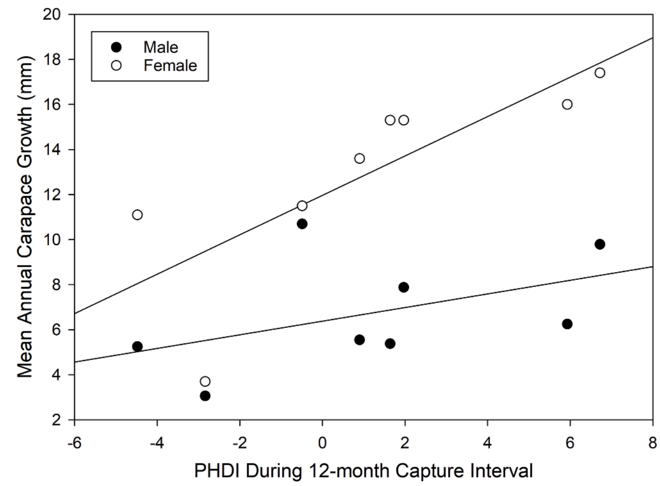

Fig. 3. Relationship for male (dark circle) and female (open circle) painted turtles between the mean, discrete annual growth in carapace length (G) and the Palmer Hydrologic Drought Index in southwestern Nebraska during the 12 months prior to capture. Trend lines are sex-specific (test for slope greater than 0: females, P<0.0001; males, P = 0.25). Turtles were captured at a pond in Keith County, Nebraska during 2015–2016.

4. Discussion

4.1. Drought impacts

Our research has the potential to help explore the complexity by which species might respond to changes in long-term climate conditions. Anthonysamy et al. [17] reported that Blanding's turtles (*Emydoidea blandingii*) in Illinois moved to riverine habitats when wetlands dried during a drought. Water levels at our study remained relatively stable through drought conditions. Beard [26] reported that turtles in our population moved temporarily from the pond, but population size was not a function of drought conditions. The painted turtles in our sample experienced variation in sex ratio and growth related to drought conditions, which emphasizes the importance of linking terrestrial and aquatic habitats in conservation management plans. Indeed, [36] reported significant changes in water chemistry and littoral zone productivity during a severe drought that impacted southwestern pond turtles (*Actinemys pallida*) in southern California. Drought has significant impacts on ecology and food webs within ponds [37].

Realized sex ratios in a captured sample may be a function of birth ratio, differential mortality, differential emigration or immigration, or differences in the timing of maturity between sexes [38]. We suspect movement levels are low for the smaller size classes in our sample [39], and our observations of a lower proportion of males incubated during hotter, drier periods supported known dynamics of temperature-dependent sex determination in turtles [12,33]. Our study provides evidence to support a growing concern for climate change to impact population growth of turtles [40,12] because of changes to sex ratios [41].

Frazer et al. [42] suggested that global warming trends had the

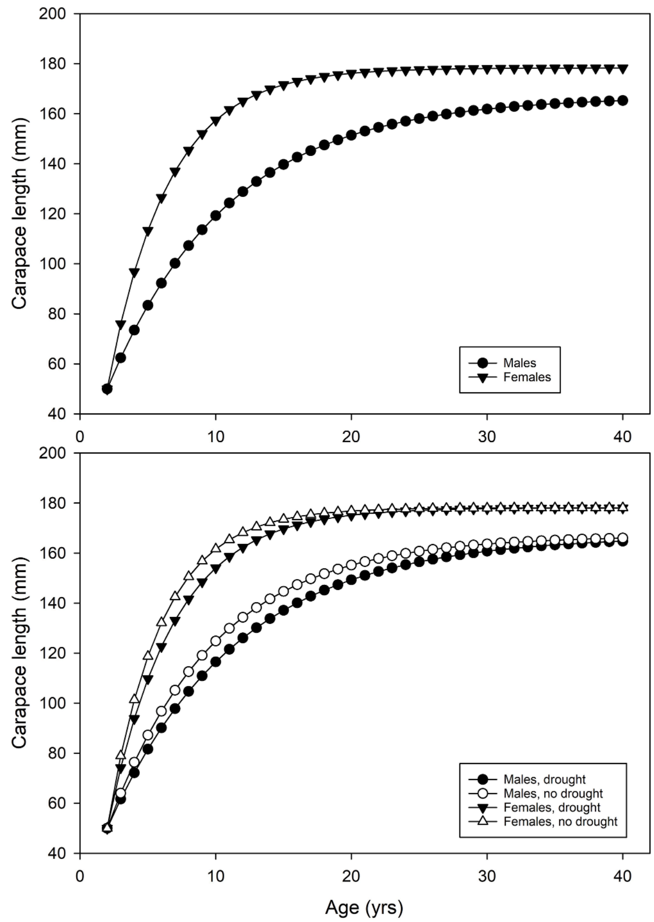

Fig. 4. Predicted growth-age curves for painted turtles captured and recaptured in a pond in Keith County, Nebraska during 2005–2016. Predictions based on 50 mm size at age two, and von Bertalanffy growth model coefficients were estimated from marked individuals. Top: predicted growth of male (circle) and female (triangle) painted turtles. Bottom: predicted growth of males and females when incorporating a drought coefficient (D) assuming turtles grew in constant drought (solid marker) or non-drought (open marker) conditions.

Table 1
Growth parameters estimated (SE, 95% confidence interval) under the von Bertalanffy model for male and female painted turtles from a pond in western Nebraska during 2005–2016 in drought and nondrought years where k is growth rate, L∞ is asymptotic size, and D is drought effect.

Model parameters	Parameter estimates	SE	95% CI
Males:			
k	0.1278	0.0115	0.1051, 01,505
L∞	166.9	2.2	162.4, 171.5
D	−0.0226	0.0108	−0.0438, −0.00134
Females:			
k	0.1977	0.0331	0.1321, 0.2633
L∞	193.9	9.3994	175.3, 212.5
D	−0.0393	0.0169	−0.0727, −0.00585

potential to increase metabolism and growth rates of pond turtles, although they did not consider the potential for increased drought conditions during global warming. Indeed, climate models predict that Nebraska and the central Great Plains will experience increasing temperatures and an increasing frequency, severity, and duration of droughts due to climate change [43]. Our results indicate drought conditions limit painted turtle growth, likely caused by limited food resources. Aquatic insects provide a high-protein diet required by egg-laying female turtles, and availability of high-protein diet items has potential to influence growth [44]. Insect abundance decreases during droughts; likewise, climate change in the Great Plains has potential to result in lower arthropod abundance [45]. We did not measure food resources during our study, but we found the PHDI, which incorporates soil moisture and temperature, to be a useful indicator of the variation in environmental conditions. Beard [26] reported reduction in annual survival during droughts for the turtles in our sample, emphasizing the direct and indirect manner by which drought may impact turtle populations.

Periods of drought with slower growth have potential to lower lifetime reproductive potential for individual turtles [20]. Our growth model predicted that females and males take longer to reach size for sexual maturity during constant drought conditions (Fig. 4). We found proportionately more females produced during extreme drought conditions. However, those females may take longer to reach sexual maturity, making the impact of climate on a population's productivity complex.

4.2. Growth models

Painted turtles are sexually dimorphic in size [23,46], and our work contributes to comparisons of sex-specific growth rates using repeated measures during long-term studies [47,48]. Females at our study site reached longer asymptotic lengths and grew at double the annual growth rate of males. Our data support the hypothesis that female turtles put energy into growth early to arrive at the size needed for sexual maturity with slower rates of growth as females put their energy into egg production and development [16].

Our model predictions for growth over time are consistent with field observations by Ernst and Lovich [23]. For example, females in our sample were predicted to reach carapace lengths for sexually mature females [23] of 120–140 mm by the ages of 5 and 7 years (Fig. 4); Ernst and Lovich [23] suggested most female painted turtles reach that size range by age 6–12. Males in our sample reached carapace lengths of 70–95 mm by ages of 3 to 5 years, which was also consistent with Ernst and Lovich [23]. Further, the validation analyses confirmed our growth model's ability to satisfactorily predict the size of unknown age painted turtles in our sample, and we suggest the resulting growth curves can be used to estimate age of turtles at our study site. The von Bertalanffy model is commonly used to predict growth of fish and subsequently predict age from size [49,34]. Given that biologists cannot age individuals of many turtle species by external examination [50], the technique we describe has potential for use in other turtle populations. The length measurements needed for these analyses are often collected in closed or open population mark-recapture studies of turtles.

5. Conclusions

Painted turtles are slow-growing, relatively long-lived species that can be affected by environmental dynamics on large temporal scales. Evidence suggests that the Great Plains will be at higher risk for drought conditions in the future, and our local study of a large population of turtles over 12 years of drought and nondrought periods has potential to inform how pond turtles may respond to warmer, drier periods in the future. We provide direct evidence that short periods of drought conditions cause reduction in growth rates. Our results may inform conservation plans for other species of turtles during dynamic climate conditions.

Data statement

The data used in this paper are available under Attribution-NonCommercial-ShareAlike 4.0 International (CC BY-NC-SA 4.0) license at: https://doi.org/10.32873/unl.dr.20221216

CRediT authorship contribution statement

Larkin A. Powell: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Ellen P. Dolph:** Formal analysis, Funding acquisition, Writing – original draft. **Charrissa R. Neil:** Formal analysis, Funding acquisition, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The manuscript contains a data availability statement with a link to the data used.

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