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# Juvenile American Alligators (*Alligator mississippiensis*) Use Behavioral Thermoregulation to Cope with Dehydration and Salt-Loading when Chronically Exposed to 12 ‰ Saltwater

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**Citation** – Faulkner, P. C., Hala, D., Shimskie, J., Johnson, R., Schneider, A., Cabbage, T., Lozano, N., & Petersen, L. H. (2023). Juvenile American alligators (*Alligator mississippiensis*) use behavioral thermoregulation to cope with dehydration and salt-loading when chronically exposed to 12‰ saltwater. *Animal Behavior and Cognition*, 10(1), 1-13. <https://doi.org/10.26451/abc.10.01.01.2023>

**Abstract** – American alligators (*Alligator mississippiensis*) are native to freshwater habitats in the Southeastern United States. These areas are susceptible to salinity increases due to extreme weather events (e.g., hurricanes) and climate change. The goal of this study was to investigate behaviors in juvenile alligators exposed to 12‰ saltwater for five weeks. Sixteen alligators were maintained in an experimental tank with 90 L of water and a heat lamp overhanging a basking plate. Observations were conducted in freshwater (prior to exposure to saltwater) and over the course of 5 weeks in 12‰ saltwater. This allowed for comparison of behaviors in freshwater and in saltwater in the same group of animals. Behaviors related to thermoregulation (basking and staying in the water) and feeding were recorded via instantaneous sampling, in which sampling intervals of 1 min occurred throughout a 20 min observation period. Saltwater-exposed alligators reduced foraging and feeding within the first week of saltwater exposure and spent significantly less time basking compared with freshwater observations. Furthermore, significantly fewer animals chose to bask over the course of 5 weeks in saltwater. A novel behavior, never seen in freshwater, was the closing of the outer eyelids when alligators were in the saltwater. Collectively, the present study demonstrates that chronic saltwater exposure has significant impact on the thermoregulatory behavior in juvenile alligators concomitantly exposed to dehydration and salt-loading without access to freshwater. As alligator hatchlings emerge during peak hurricane season, the survivability of hatchlings may be compromised if access to freshwater is unattainable.

**Keywords** – American alligator, Saltwater, Behavior, Thermoregulation, Basking, Feeding

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American alligators [*Alligator mississippiensis* (Daudin, 1802)] are native to the Southeastern United States and inhabit mainly freshwater areas. Although large individuals are known to forage in brackish water, and some have even been reported foraging in estuarine and marine saltwater areas (Elsey, 2005; Fujisaki et al., 2014; Rosenblatt & Heithaus, 2011), alligators prefer low saline environments or need frequent access to freshwater if foraging in saline environments (Fujisaki et al., 2014; Jacobsen, 1983). Many alligator populations live in coastal wetlands that are vulnerable to salinity increases via sea level rise and hurricane-induced storm surges. Storm surges push seawater into coastal freshwater areas, causing short- or long-lasting saline environments, which can impact alligator movement (Jackson et al., 1995; Michener et al., 1997; Schriever et al., 2009; Strickland et al., 2020). Increases in salinity can additionally stem from months with low rainfall, which enhance the concentration of salts and solutes as freshwater evaporates (Lance et al., 2010). Furthermore, gradual changes in climate result in subtle but persistent

salinity changes that are not likely reversible. The International Panel on Climate Change (IPCC) predicts that by the end of the 21<sup>st</sup> century sea levels will rise by 28-48 cm above levels at the beginning of the century, causing saline environments in coastal freshwater habitats. Sea level rise is not only a concern for surface coastal waters, but it can also introduce saline water into inland groundwater fed wetlands, resulting in salinization of further inland areas (Wood & Harrington, 2015). Indeed, recent predictions estimated that considerable areas of wetlands will be lost from the Mississippi River Delta by 2050 (Barras et al., 2003, 2008). Finally, increased sea surface temperatures in the tropics (e.g., 1°C over the past century) are correlated with increased hurricane intensity, as shown by an increase in category 4 and 5 hurricanes (DeLaune & White, 2012; Emanuel, 2005; Hoyos et al., 2006), with ensuing increased frequency in storm surges.

The hurricane season in the Southeastern United States ranges from June-November, with most large hurricanes forming in the months of August and September (Curtis, 2008; Saunders & Lea, 2005). This overlaps with the reproductive season of American alligators, as eggs hatch in the months of July and August (Joanen, 1969; Lance, 1989). Emergence of hatchlings therefore coincides with peak hurricane season. In contrast to crocodiles, alligators do not possess lingual salt glands and are consequently unable to regulate electrolytes (Na<sup>+</sup>, Cl<sup>-</sup>) in hyperosmotic conditions (Faulkner et al., 2018, 2019, 2021; Laurén, 1985; Pidcock et al., 1997; Taplin, 1988). While lack of salt glands prevents excretion of excessive Na<sup>+</sup> and Cl<sup>-</sup> ions, the permeable integument fails to prevent diffusive loss of body water to external saline environments and the influx of ions (Ellis & Evans, 1984; Mazzotti & Dunson, 1984; Taplin et al., 1982). Elevated salinity levels, therefore, result in dehydration and increased plasma electrolyte levels (Faulkner et al., 2018, 2019; Laurén, 1985; Pidcock et al., 1997; Taplin, 1988). As cutaneous evaporative water loss per body mass increases as body size decreases (Davis et al., 1980), young alligators are at higher risk of dehydration during salinization events. Furthermore, the activity rates (e.g., moving to more favorable environments) of adult alligators increase when salinity levels rise (Fujisaki et al., 2014), but as young alligators stay in alligator “pods” for the first year of life (Woodward et al., 1987) they may not disperse as easily as older alligators when salinity levels increase.

Laboratory-based studies on juvenile alligators (1-2 years old) have demonstrated that 12‰ saltwater resulted in elevated stress hormones (corticosterone and 11-deoxycortisol) (Faulkner et al., 2018, 2019), dehydration, and significantly increased levels of plasma electrolytes (Na<sup>+</sup>, Cl<sup>-</sup>) and osmolality (Faulkner et al., 2018, 2019; Lance et al., 2000, 2010; Laurén, 1985; Morici et al., 1997) compared with levels measured in alligators maintained in freshwater. As physiological function commonly influences behavior (Blüm & Fiedler, 1965; Fitzsimons, 1998), it is likely that physiological changes associated with salinity stress (dehydration, salt-loading) alter behaviors in juvenile alligators. For instance, the lizard *Sceloporus undulatus*, desert iguana (*Dipsosaurus dorsalis*), and agamid lizard (*Ctenophorus ornatus*) reduce their resting body temperatures during dehydration and hypernatremia (Crowley, 1987; Bradshaw et al., 2007; Dupré & Crawford, 1985). The thermoregulatory responses to dehydration and salt-loading in reptiles seems to be a strategy to minimize evaporative water loss but consequently reduces activity (Bradshaw et al., 2007; Ladyman et al., 2006). Although wild alligators seem to increase activity by leaving high salinity areas (Fujisaki et al., 2014), alligators have been observed to burrow or even aestivate if movement to a freshwater environment is restricted (Taplin, 1988). These methods of water conservation can potentially come at the cost of reducing important routine activities, such as foraging or reproductive behaviors. Because alligators are considered a keystone species due to their impacts on local plants and animals, salinization of freshwater wetlands can have significant negative ecosystem level effects (Mazzotti et al., 2009; Mazzotti & Brandt, 1994). To target restoration and conservation efforts, it is therefore imperative to have a comprehensive knowledge of how salinization impacts alligator physiology and behavior.

The goal of the present study was to assess behavioral changes in juvenile alligators exposed to low salinity water (12‰). Our specific aim was to observe any water conservation behaviors displayed by juvenile alligators unable to seek refuge in a freshwater environment. Since salinization events are unpredictable and environmental observations are often confounded by many factors, the current study used a laboratory-based investigation to assess juvenile alligator feeding (looking for food, ingesting food), and

basking (spending time on the basking plate) behaviors when animals were chronically (5 weeks) exposed to saltwater (12‰). Based on previous studies on saltwater effects on food intake and osmoregulation in freshwater reptiles (Bower et al., 2016; Faulkner et al., 2018; Laurén, 1985; Morici, 1996), and studies on behavioral thermoregulation in reptiles exposed to dehydration or osmotic loading (Dupré & Crawford, 1985; Ladyman & Bradshaw, 2003; Rozen-Rechels et al., 2019), we hypothesized that in the absence of access to freshwater, alligators exposed to saltwater would seek refuge in the water to lower their body temperature and reduce feeding. Behaviors related to water conservation will be described below.

## Method

### Ethics Statement

All research met humane standards and was approved by Texas A&M University's Institutional Animal Care and Use Committee (IACUC AUP 2015-0347).

### Animals and Husbandry

Juvenile American alligators (1-2 years old; average body mass  $639 \pm 40.3$  g; snout-vent length  $29.5 \pm 0.65$  cm) were generously donated by Rockefeller Wildlife Refuge (Louisiana, USA) and transported to Texas A&M University at Galveston, Texas, USA (TPWD SPR-0416-097). Alligators were housed under a photoperiod (12:12 light:dark cycle) in a temperature-controlled room, which maintained air temperature at  $26 \pm 1^\circ\text{C}$  both during light and dark hours. A 160 W UVB light heat lamp (Zoo Med Laboratories, Inc.) provided heat and UVB rays directly over the basking plate (35.5 cm X 35.5 cm), resulting in basking plate temperatures averaging  $26.00 \pm 0.79^\circ\text{C}$ . Twenty five percent of the tank was covered by a dark tarp to allow animals to shelter. Air temperature away from the heat lamp ranged  $25\text{-}26^\circ\text{C}$  and water temperature underneath the shade and in the open area of the tank averaged  $24.14 \pm 0.46^\circ\text{C}$ . The experimental set-up allowed for a thermogradient between the basking plate temperature and that of the water.

Animals were kept at a stocking density of 16 animals in a 380 L Rubbermaid stock tank (Rubbermaidcommercial.com) containing 90 L of freshwater. Animals were fed an average of 3% body mass per week of Mazuri<sup>®</sup> Reptile Diet (PMI Nutrition International). Food intake of alligators was closely monitored by counting pellets and food was continuously offered three times a week during the study. Complete water changes were performed 24-30 hr after each feeding (three per week). Animals were maintained in freshwater cultures for approximately 6 months prior to experimentation. Upon completion of this study, eight alligators were sampled for a concurrent study (Faulkner et al., 2018) while the remaining eight were returned to freshwater and used for subsequent preliminary studies.

### Experimental Design

The present study was part of a concurrent study on the effects of chronic saltwater exposure on juvenile alligator physiology and endocrinology (Faulkner et al., 2018). As per Faulkner et al. (2018), the salinity concentration was based on previous studies in which juvenile alligators were exposed to salinity levels up to 18‰ and 20‰ (Laurén, 1985; Morici, 1996). However, these studies observed mortality at levels higher than 14‰, but reported 8‰ as being iso-osmotic to alligator plasma, with 10‰ and above being hyperosmotic (Laurén, 1985; Morici, 1996). To ensure salinity effects while avoiding mortalities, we used 12‰ as the highest salinity level. Chlorine was removed by keeping tap water in stock tanks for two days before each water change. Water quality test strips (LaMotte Inc., Chestertown, MD, USA) were subsequently used to confirm chlorine was absent in stock tanks at the time of water change. The saltwater treatment group was gradually exposed to increasing salinity levels over eight days, during which salinity was increased every two days from 0‰ to 4‰, to 8‰, and finally to 12‰ for the duration of the experiment. Saltwater was obtained by mixing freshwater with filtered and sterilized seawater from the Gulf of Mexico

off Galveston Island, Texas, USA to achieve 12‰. Throughout the present study, salinity levels in stock and exposure tanks [saltwater (12‰)] were measured with a salinity meter (Oakton Instruments, WD-35604-00) twice daily.

### **Behavioral Observations**

Alligators stay together in “pods” for at least their first year of life (Woodward et al., 1987) and hence the group observations of the 16 animals simulated “pod” behavior. The alligators were filmed under two conditions: remotely without the presence of people and during feeding events. Three main categories of alligator behaviors were determined: “water”, “basking”, and “feeding”. To avoid changes in behavioral responses due to observer presence, “water” and “basking” behavior observations were always conducted using video recordings using a Canon EOS Rebel T2i (18.0 megapixel) camera positioned on a tripod. This allowed for observations of all 16 alligators in the tank at one time. Each video segment was filmed in 20 min intervals 2-3 times a day, on days the animals were not fed, 3 times per week. “Water” behaviors included behaviors only observed when animals were left undisturbed and postabsorptive (+24 hours since last feeding) and when the alligators were observed in the water. “Basking” behavior was similarly determined when animals were undisturbed and included observations on the basking plate only. Thus, these behaviors were mutually exclusive and represented the only two states that we recorded. However, we observed an “eye closed” behavior when alligators were sitting in saltwater, and have therefore included this behavior in our observations and analyzes.

The “feeding” behavior observations occurred during the feeding events. Feeding behaviors included behaviors observed during the feeding events. “Foraging” was characterized by alligators looking for food pellets, either in the water or on the basking plate, and “feeding” included behaviors such as grabbing and ingesting the pellets. Feeding behaviors were filmed in 20 min segments on feeding days (3 times a week). Feeding events were always video recorded in the presence of investigators. However, alligators used in the present study were in the laboratory facility for at least 6 months prior to experimentation and were thus used to investigator presence during feeding.

All video recordings were performed two weeks prior to treatment (in freshwater) and during the 5-week saltwater exposure study. Thus, observations ranged a total of seven weeks. All observations were conducted in the timeframe of 8am-5pm and, to account for diurnal differences recordings of “water” and “basking” behaviors, were randomly selected from different days and different times of the day with a minimum of 6 observations per week. Feeding observations averaged three per week and thus all were included for analysis.

### **Data Collection and Statistical Analyses**

Behaviors were sampled by observing the entire group of 16 alligators (i.e., scan sampling). Behaviors were recorded using instantaneous sampling (Bateson and Martin, 2021) in which each sampling interval was 1 min, providing 20 sample points per observation period of 20 min. Percent time spent on a behavior was calculated as the number of sampling points in which a behavior was observed divided by the total number of sampling intervals (20). Percent number of animals included the number of animals performing the behavior divided by the total number of animals in the tank ( $N = 16$ ). Most of the data did not meet criteria for normal Gaussian distribution, and hence non-parametric tests followed by post-hoc tests were performed on all data. Percent time spent and percent number of animals were compared between freshwater exposure and each saltwater exposure week. Friedman Tests followed by Dunn’s post-hoc tests were performed to account for repeated sampling. Significance was assumed at  $p \leq 0.05$  for all data points. Statistical analyses were performed using GraphPad Prism version 5.0. All data shown in text and figures are mean  $\pm$  SEM.

Results

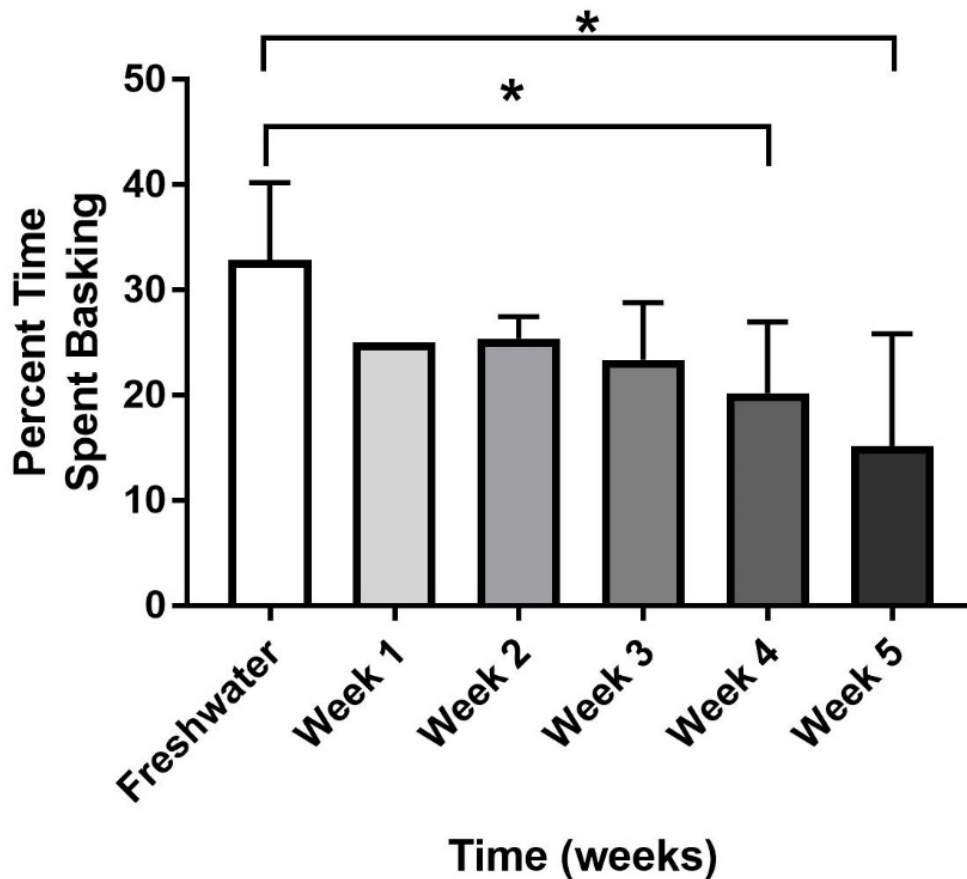
Thermoregulatory Behaviors

Exposure to 12‰ saltwater had significant effects on alligator basking behaviors. Basking time was significantly reduced ( $F_r = 15.31, p = .009$ ) as time in 12‰ saltwater increased (weeks 1 to 5) (Figure 1). On average 30.69% of the observation time was spent on basking in freshwater, but a Dunn’s test revealed that basking time was significantly reduced in weeks 4 and 5 compared with freshwater basking time (i.e., only 17.32% of alligators basked in week 5). The decrease in basking time was, however, evident already from the first week of exposure to saltwater (25.00% in week 1 vs 30.69% in freshwater) and then gradually and consistently decreased across weeks (Figure 1).

There was always at least one animal on the basking plate during freshwater exposure, however, the number of animals that basked significantly decreased ( $F_r = 11.63, p = .04$ ) as time exposed to saltwater increased (Figure 2).

Figure 1

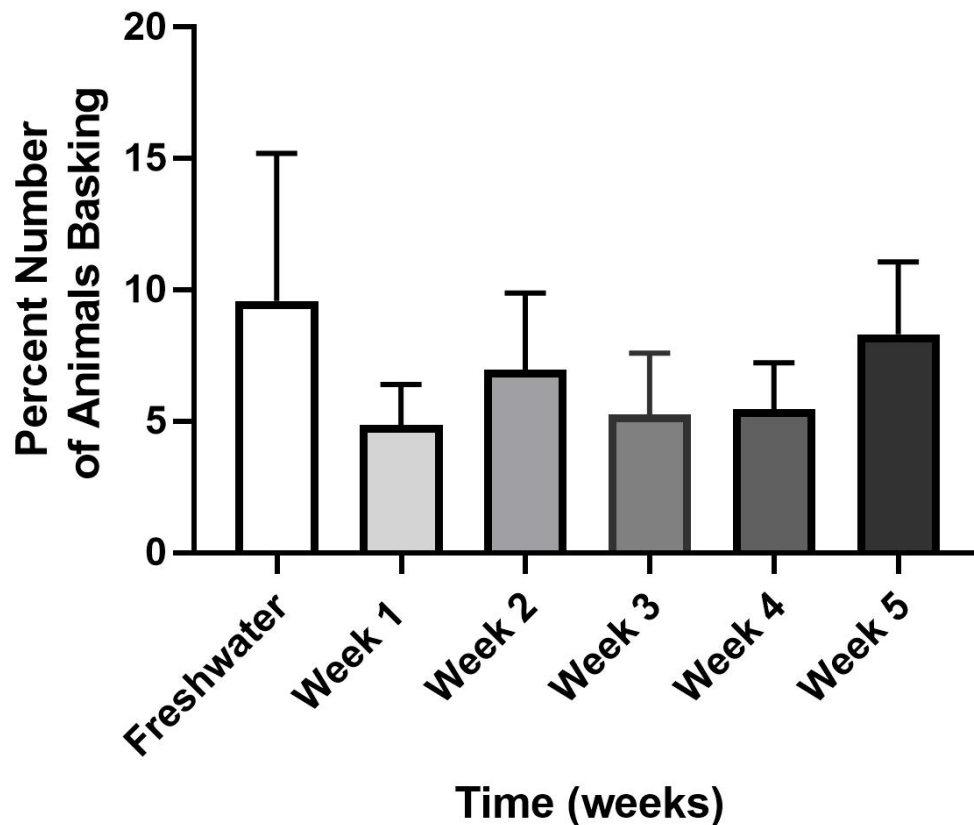
Percent of Time Alligators Spent on the Basking Plate in Freshwater and During 5-week Exposure to 12‰ Saltwater



Note. Percentages were calculated as the sum of time spent on the basking plate divided by the total time of video recording during each time interval (20 min).  $n = 16$ .

Figure 2

Percent Number of Animals on the Basking Plate in Freshwater and During 5-Week Exposure to 12‰ Saltwater



Note. The number of animals was calculated as the average number of animals on the basking plate during each time interval (20 min) divided by the total number of animals ( $n=16$ ).

One unexpected behavior seen in saltwater-exposed alligators was the presence of eyelid closure when in saltwater (Figure 3). This was a behavior that was not observed when animals were in freshwater but gradually became more prevalent over the course of saltwater exposure (Figures 3 and 4). By week 3, alligators spent significantly ( $F_r = 20.19, p = .001$ ) more time in the water with their eyelids closed (Figure 4A). Furthermore, the number of animals ( $F_r = 17.37, p = .004$ ) displaying this behavior increased significantly ( $F_r = 20.19, p = .001$ ) as time in saltwater increased (Figure 4B).

### Feeding in Fresh- and 12‰ Saltwater

Exposure to 12‰ saltwater had an immediate effect on juvenile alligator foraging and feeding behaviors. The number of animals foraging ( $F_r = 19.25, p = .002$ ) and feeding ( $F_r = 18.25, p = .003$ ) in the water was greatly reduced in the first week of saltwater exposure (Week 1) and significantly reduced by Week 4 (Figure 5A and Figure 5B). The number of alligators that searched for food pellets on the basking plate ( $F_r = 25, p < .001$ ) (Figure 5C) and feeding from the basking plate ( $F_r = 25, p < .001$ ) was significantly (Figure 5D) reduced after spending less than one week in 12% saltwater. This was despite food pellets being dropped on the plate during each feeding.

**Figure 3**

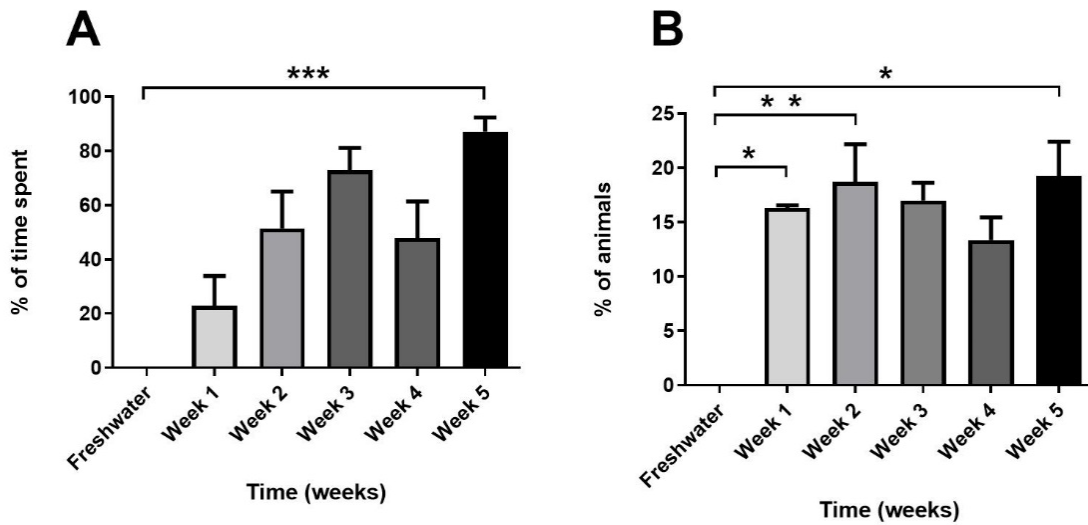
*Saltwater-Exposed Juvenile Alligators Displaying ‘Eyes Closed’ Behavior*



*Note.* Photo Credit: L.H. Petersen.

**Figure 4**

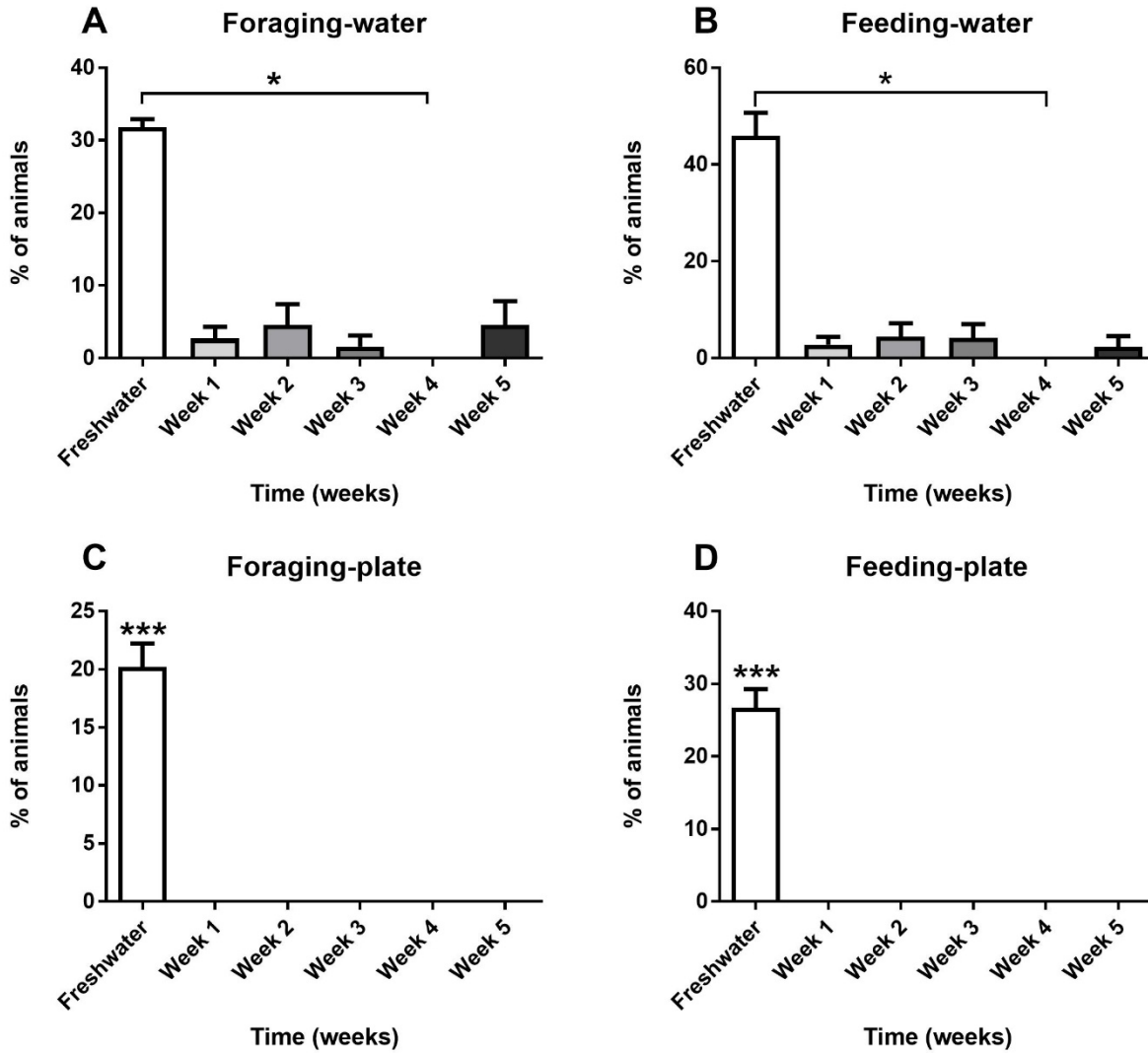
*Percent of Time Spent (A) and Percent Number of Animals (B) Displaying Eyes Closed in Freshwater and 12‰ Saltwater*



*Note.* Asterisks (\*) denotes significance at the  $p = .01$  and (\*\*) at  $p = .001$  levels.  $n = 16$ .

**Figure 5**

*Percent Number of Alligators who Looked for Food in the Water (A) and on the Basking Plate (C) and Percent Number of Alligators that Ingested the Food in the Water (B) and on the Basking Plate (D) While in Freshwater and During a 5-week Exposure to 12‰ Saltwater*



*Note.* Asterisks denote overall statistical (Friedman Test with Dunn’s post-hoc) significance between feeding behaviors observed in freshwater compared with saltwater. Data shown are mean ± SEM. *N* = 16.

**Discussion**

This study investigated how chronic (5 weeks) exposure to 12‰ saltwater impacted laboratory-kept juvenile alligator thermoregulatory behavior. Results from this study supported our research hypothesis, as alligators spent more time in the water (where temperature was lower) compared with the time on the basking plate (where temperature was higher) during saltwater exposure.

One of the most significant findings from the present study pertains to basking behaviors. Data showed that the time spent basking and the number of alligators that basked significantly decreased in the saline environment compared with freshwater. Results from this study correlate well with documented



crocodilian behavioral thermoregulation that uses adjustments of body temperature to support different physiological needs (Grigg & Seebacher, 2001; Lang, 1987). In our concurrent study, we demonstrated that saltwater exposure caused significant elevations in juvenile alligator plasma  $\text{Na}^+$  and  $\text{Cl}^-$  levels and led to significant dehydration (Faulkner et al., 2018). These physiological effects are likely to have impacted alligator thermoregulatory behavior as reported for other reptiles (Le Galliard et al., 2021; Rozen-Rechels et al., 2019; Sannolo & Carretero, 2019). For instance, dehydrated lizards (Sannolo & Carretero, 2019) and Western tiger snakes (*Notechis scutatus*) (Ladyman & Bradshaw, 2003) selected for lowered thermal spaces, which reduced their body temperature (Ladyman & Bradshaw, 2003; Sannolo & Carretero, 2019). In addition, chronic injection of sodium chloride into agamid lizards (*Ctenophorus ornatus*) that did not experience concurrent dehydration still reduced the thermal preference (Bradshaw et al., 2007). In the current study, the alligators experienced both dehydration and salt-loading and were thus challenged with two conditions that could affect behavioral thermoregulation.

The water temperature in the experimental tank was lower ( $24.14 \pm 0.46^\circ\text{C}$ ) compared with temperatures on the basking plate ( $26.00 \pm 0.79^\circ\text{C}$ ), and a dark cover was placed on one side of the tank to shield some of the water from the UVB heat lamp. Wild alligators are known to use the water to lower their body temperature (Brisbin et al., 1982; Diefenbach, 1975), and a similar strategy seemed to occur in alligators that did not have a freshwater refuge (current study) and whose only refuge from the saltwater was the warmer basking plate. Behavioral thermoregulation is commonly used in American alligators after feeding to aid in digestion (Lang 1979) and to regulate enzyme activities in summer and winter months to compensate for the lower or higher environmental temperatures (Seebacher, 2005; Seebacher, Guderley et al., 2003; Seebacher, Elsey et al., 2003). Alligators in the current study may have used similar metabolic compensation strategies to decrease the rate at which body water was lost to the saline environment. Spending more time in the water would therefore have alleviated metabolic-associated cutaneous and respiratory water loss, as both are positively correlated with body temperatures in alligators (Davis et al., 1980).

While spending more time in the water may have reduced body temperature and slowed down dehydration, it seems a contradictory strategy; more time spent in saltwater would increase the influx of electrolytes ( $\text{Na}^+$ ,  $\text{Cl}^-$ ) as alligator integument is not impermeable to ion fluxes (Ellis & Evans, 1984; Mazzotti & Dunson, 1984; Taplin et al., 1982). One novel behavior that was never observed in freshwater was alligators closing the outer eyelids when sitting immobile in the saltwater. Alligators have an upper and lower eyelid, in addition to a third nictitating membrane that is transparent and enables the animal to see underwater (Rehorek et al., 2005). Alligators in saltwater began showing signs of closing the outer eyelid as early as the first week of exposure (Figure 4) and the occurrence of this behavior significantly increased with time, peaking during week 5. Closing the outer eyelid is usually a protective measure to protect the eye during prey capture (Kerfoot et al., 2016). However, mucus membranes in eyes, nostrils, mouth, or vent provide a thinner barrier through which ions can be exchanged between the body and environment (Taplin, 1985). Thus, closing the eyelid seemed to be a protective measure to prevent influx of ions ( $\text{Na}^+$ ,  $\text{Cl}^-$ ) when alligators were in saltwater. This strategy was likely a result of the inability of alligators to seek a freshwater refuge during the experiment. Selecting a lower thermal space (saltwater) likely acted as a dual strategy to 1) lower the rate of dehydration and 2) lower the rate of metabolic processes in an attempt to maintain osmoregulatory homeostasis. Observations further showed that alligators became less active as time in saltwater increased (Faulkner and Petersen, personal observations), correlating well with the behavior of wild alligators seeking a more favorable microhabitat, which can include burrowing or even aestivation, if movement to a freshwater environment is restricted (Taplin, 1988).

The selection of lower thermal environment, albeit this being a saline environment, was further evident in the alligators' feeding behaviors. Depressed feeding behaviors (grabbing food pellets, foraging, actively feeding) were observed at the onset of saltwater exposure where foraging for pellets and actively feeding from the water were greatly reduced, while feeding from the basking plate was completely absent starting from the first week of saltwater exposure. Other studies on laboratory-kept juvenile alligators exposed to various salinity levels have demonstrated similar effects of salinity on feeding and food intake (Faulkner et al., 2018, 2019; Laurén, 1985). When exposed to elevated saline environments crocodilians

display selective drinking and feeding behavioral strategies (Taplin, 1988) but as there are osmoregulatory differences between the Alligatorid and Crocodylid families (Taplin, 1988; Taplin et al., 1982) food intake is differently affected. For example, American crocodiles (*Crocodylus acutus*) maintained in 10‰ continued feeding and even rapidly gained weight, and when exposed to 18‰ they still gained weight, albeit at a slower rate (Dunson, 1982). Other freshwater reptiles display different strategies. For instance, freshwater turtles (*Chelodina expansa* and *Emydura macquarii*) exposed to 15‰ saltwater for 50 days ceased to feed, which was considered a behavioral response to reduce salt intake in order to further limit dehydration (Bower et al., 2016). It is unlikely, however, that juvenile alligators in the present study refused feeding due to reducing salt intake, as they were given a commercially available reptilian diet rather than feeding on live prey, which could have higher salt content. The reduced feeding was more likely correlated with the thermoregulatory behavior and the physiological changes experienced by the alligators. Feeding is followed by digestion which, in ectotherms, necessitates the elevation of body temperature to accommodate digestive processes and therefore involves finding areas with higher temperatures (Blouin-Demers & Weatherhead, 2001; Gatten, 1974; Slip & Shine, 1988). Recently fed alligators are known to select for higher temperature environments (Lang, 1979), which decreases gastric residence time (Diefenbach, 1975), while fasted alligators select lower temperatures (Lang, 1979). The salt-loading experienced by the alligators drove the selection for a lower thermal environment but feeding would have necessitated selecting a higher temperature. The advantage of selecting a lower thermal environment is that it concurrently decreased metabolic processes and, thereby, the need to feed, so the lowered feeding rate seems to be a consequence of the behavioral thermoregulation that was aimed at alleviating the physiological changes occurring in the alligators (Faulkner et al., 2018). Behavioral thermoregulation aimed to suppress the rates of dehydration and ionic influxes would, however, have exacerbated the water loss, as many animals depend on metabolic water from food items (Willmer et al., 2009). Therefore, reduced feeding could have attributed to the significant dehydration.

### Conclusion

In conclusion, this study showed that when juvenile alligators are concomitantly challenged with dehydration and salt-loading, they select for lower thermal microhabitats. As dehydration or hypernatremia lead to lower thermal preference in various lizard species (Bradshaw et al., 2007; Sannolo & Carretero, 2019), the combined effects of dehydration and salt-loading would both have influenced the thermoregulatory behavior of the juvenile alligators. However, as alligators differ from other reptiles, future studies should investigate the underlying mechanisms that drive the behavioral thermoregulation observed in the current study. Furthermore, the novel finding that saltwater exposed alligators closed the outer eyelids warrants further study to delineate the underlying regulatory or behavioral mechanisms.

Collectively, this study showed that salinization events can have negative impacts on body condition, growth, and health of juvenile alligators, as alligators will select for lower thermal environments which reduce metabolic processes. Results from laboratory studies facilitate knowledge of how future storm surges or droughts affect alligator physiology and behavior and are pertinent in targeting restoration efforts for vulnerable alligator populations impacted by current and future salinization events.

### Acknowledgements

We are grateful to Dr. Ruth Elsey and staff at Rockefeller Wildlife Refuge, LA for donating juvenile alligators and for their support and advice. We are further grateful to Katie St. Clair and student workers for helping with alligator husbandry.

**Funding:** This work was funded from start-up funds to L.H.P. and D.H. from Texas A&M University.

**Data Availability:** The data that support the findings of this study are available upon request from the corresponding author.

**Conflict of Interest:** The authors declare no conflict of interest.

**Author Contributions:**

**PF:** Methodology, Data curation, Writing – Original draft, Writing – Reviewing and Editing. **DH:** Supervision, Writing – Original draft, Writing – Reviewing and Editing. **JS:** Data curation, Validation. **RJ:** Data curation, Validation. **AS:** Data curation, Validation. **TC:** Data curation, Validation. **NL:** Data curation, Validation. **LHP:** Conceptualization, Methodology, Supervision, Data curation, Writing – Original draft preparation; Writing – reviewing and editing, Project administration.

**References**

- Barras, J. A., Bernier, J. C., & Morton, R. A. (2008). *Land area change in coastal Louisiana, a multidecadal perspective (from 1956 to 2006)*: US Department of the Interior, US Geological Survey Louisiana, US.
- Barras, J. A., Beville, S., Britsch, D., Hartley, S., Hawes, S., Johnston, J., Kemp, Kinler, Q. Martucci, A., Porthouse, J., Reed, D. Roy, K., Sapkota, S., & Suhayda, J. (2003). *Historical and projected coastal Louisiana land changes: 1978-2050*: United States Geological Survey Louisiana, US.
- Bateson, M., & Martin, P. (2021). *Measuring Behaviour: An Introductory Guide*. Cambridge University Press.
- Blouin-Demers, G., & Weatherhead, P. J. (2001). Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology*, 82(11), 3025–3043.
- Blüm, V., & Fiedler, K. (1965). Hormonal control of reproductive behavior in some cichlid fish. *General and Comparative Endocrinology*, 5(2), 186–196.
- Bower, D. S., Scheltinga, D. M., Clulow, S., Clulow, J., Franklin, C. E., & Georges, A. (2016). Salinity tolerances of two Australian freshwater turtles, *Chelodina expansa* and *Emydura macquarii* (*Testudinata: Chelidae*). *Conservation Physiology*, 4(1), cow042.
- Bradshaw, D., Ladyman, M. and Stewart, T. (2007). Effect of hypernatraemia and the neurohypophysial peptide, arginine vasotocin (AVT) on behavioural thermoregulation in the agamid lizard, *Ctenophorus ornatus*. *General and comparative endocrinology*, 150(1), 34–40.
- Brisbin Jr, I. L., Standora, E. A., & Vargo, M. J. (1982). Body temperatures and behavior of American alligators during cold winter weather. *American Midland Naturalist*, 209–218.
- Crowley, S. R. (1987). The effect of desiccation upon the preferred body temperature and activity level of the lizard *Sceloporus undulatus*. *Copeia*, 25–32.
- Curtis, S. (2008). The Atlantic multidecadal oscillation and extreme daily precipitation over the US and Mexico during the hurricane season. *Climate Dynamics*, 30(4), 343–351.
- Davis, J. E., Spotila, J. R., & Scheffler, W. C. (1980). Evaporative water loss from the American alligator, *Alligator mississippiensis*: The relative importance of respiratory and cutaneous components and the regulatory role of the skin. *Comparative Biochemistry and Physiology Part A: Physiology*, 67(3), 439–446.
- Daudin, F. M. (1802). *Histoire naturelle, générale et particulière des reptiles: ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par CS Sonnini, membre de plusieurs sociétés savantes* (Vol. 2): Dufart.
- DeLaune, R., & White, J. R. (2012). Will coastal wetlands continue to sequester carbon in response to an increase in global sea level?: A case study of the rapidly subsiding Mississippi river deltaic plain. *Climatic Change*, 110(1), 297–314.
- Diefenbach, C. O. D. C. (1975). Thermal preferences and thermoregulation in *Caiman crocodilus*. *Copeia*, 530–540.
- Dunson, W. A. (1982). Salinity relations of crocodiles in Florida Bay. *Copeia*, 374–385.
- Dupré, R.K., & Crawford Jr, E.C. (1985). Behavioral thermoregulation during dehydration and osmotic loading of the desert iguana. *Physiological zoology*, 58(4), 357–363.
- Ellis, T. M., & Evans, D. H. (1984). Sodium balance in the American alligator. *Journal of Experimental Zoology*, 231(3), 325–329.
- Elsy, R. M. (2005). Unusual offshore occurrence of an American alligator. *Southeastern Naturalist*, 4(3), 533–536.
- Emanuel, K. (2005). Increasing destructiveness of tropical cyclones over the past 30 years. *Nature*, 436(7051), 686.

- Faulkner, P., Burlison, M., Simonitis, L., Marshall, C., Hala, D., & Petersen, L. (2018). Effects of chronic exposure to 12‰ saltwater on the endocrine physiology of juvenile American alligator (*Alligator mississippiensis*). *Journal of Experimental Biology*, 221(Pt 14), jeb181172.
- Faulkner, P. C., Hala, D., Rahman, M. S., & Petersen, L. H. (2019). Short-term exposure to 12‰ brackish water has significant effects on the endocrine physiology of juvenile American alligator (*Alligator mississippiensis*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 236, 110531.
- Faulkner, P. C., Elsey, R. M., Hala, D., & Petersen, L. H. (2021). Correlations between environmental salinity levels, blood biochemistry parameters, and steroid hormones in wild juvenile American alligators (*Alligator mississippiensis*). *Scientific Reports*, 11(1), 1–13.
- Fitzsimons, J. (1998). Angiotensin, thirst, and sodium appetite. *Physiological reviews*, 78(3), 583–686.
- Fujisaki, I., Hart, K. M., Mazzotti, F. J., Cherkiss, M. S., Sartain, A. R., Jeffery, B. M., Beauchamp, J. S., & Denton, M. (2014). Home range and movements of American alligators (*Alligator mississippiensis*) in an estuary habitat. *Animal Biotelemetry*, 2(1), 1–10.
- Gatten Jr, R. E. (1974). Effect of nutritional status on the preferred body temperature of the turtles *Pseudemys scripta* and *Terrapene ornata*. *Copeia*, 912–917.
- Grigg, G., & Seebacher, F. (2001). Crocodylian thermal relations. *Crocodylian Biology and Evolution*. Cornell University Press.
- Hoyos, C. D., Agudelo, P. A., Webster, P. J., & Curry, J. A. (2006). Deconvolution of the factors contributing to the increase in global hurricane intensity. *Science*, 312(5770), 94–97.
- Jacobsen, T. (1983). Crocodylians and islands: Status of the American alligator and the American crocodile in the lower Florida Keys. *Florida Field Naturalist*, 11, 1–24.
- Jackson, L. L., Foote, A. L., & Balistrieri, L. S. (1995). Hydrological, geomorphological, and chemical effects of hurricane Andrew on coastal marshes of Louisiana. *Journal of Coastal Research*, 306–323.
- Joanen, T. (1969). *Nesting ecology of alligators in Louisiana* [Paper Presentation]. Proceedings of the Southeastern Fish and Wildlife Conference.
- Kerfoot, J. R., Easter, E., & Elsey, R. M. (2016). How doth the little crocodylian: Analyzing the influence of environmental viscosity on feeding performance of juvenile *Alligator mississippiensis*. *Biology*, 5(4), 36.
- Ladyman, M., & Bradshaw, D. (2003). The influence of dehydration on the thermal preferences of the Western tiger snake, *Notechis scutatus*. *Journal of Comparative physiology B*, 173(3), 239–246.
- Ladyman, M., Bradshaw, D. & Bradshaw, F. (2006). Physiological and hormonal control of thermal depression in the tiger snake, *Notechis scutatus*. *Journal of Comparative Physiology B*, 176, 547–557.
- Lance, V. A. (1989). Reproductive cycle of the American alligator. *American Zoologist*, 29(3), 999–1018.
- Lance, V. A., Elsey, R. M., Butterstein, G., Troclair III, P. L., & Merchant, M. (2010). The effects of Hurricane Rita and subsequent drought on alligators in southwest Louisiana. *Journal of Experimental Zoology*, 313, 106–113.
- Lance, V. A., Morici, L. A., & Elsey, R. M. (2000). Physiology and endocrinology of stress in alligators. In G. C. Grigg, F. Seebacher, & C. E. Franklin (Eds.), *Crocodylian Biology and Evolution* (pp. 327–340). Surrey Beatty and Sons.
- Lang, J. W. (1979). Thermophilic response of the American alligator and the American crocodile to feeding. *Copeia*, 48–59.
- Lang, J. W. (1987). Crocodylian thermal selection. *Wildlife Management: Crocodiles and Alligators*, 301, 317.
- Laurén, D. J. (1985). The effect of chronic saline exposure on the electrolyte balance, nitrogen metabolism, and corticosterone titer in the American alligator, *Alligator mississippiensis*. *Comparative Biochemistry and Physiology Part A: Physiology*, 81(2), 217–223.
- Le Galliard, J.F., Rozen-Rechels, D., Lecomte, A., Demay, C., Dupoué, A., & Meylan, S., 2021. Short-term changes in air humidity and water availability weakly constrain thermoregulation in a dry-skinned ectotherm. *Plos one*, 16(2), p.e0247514.
- Mazzotti, F. J., Best, G. R., Brandt, L. A., Cherkiss, M. S., Jeffery, B. M., & Rice, K. G. (2009). Alligators and crocodiles as indicators for restoration of Everglades ecosystems. *Ecological Indicators*, 9(6), S137–S149.
- Mazzotti, F. J., & Brandt, L. A. (1994). Ecology of the American alligator in a seasonally fluctuating environment. In *Everglades: The Ecosystem and its Restoration* (pp. 485–505).
- Mazzotti, F. J., & Dunson, W. A. (1984). Adaptations of *Crocodylus acutus* and alligator for life in saline water. *Comparative Biochemistry and Physiology Part A: Physiology*, 79(4), 641–646.
- Michener, W. K., Blood, E. R., Bildstein, K. L., Brinson, M. M., & Gardner, L. R. (1997). Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications*, 7(3), 770–801.

- Morici, L. (1996). *Endocrine and physiological response to osmotic stress in the American Alligator, Alligator mississippiensis*. University of San Diego.,
- Morici, L. A., Elsey, R. M., & Lance, V. A. (1997). Effects of long-term corticosterone implants on growth and immune function in juvenile alligators, *Alligator mississippiensis*. *Journal of Experimental Zoology*, 279(2), 156–162.
- Pidcock, S., Taplin, L., & Grigg, G. (1997). Differences in renal-cloacal function between *Crocodylus porosus* and *Alligator mississippiensis* have implications for crocodylian evolution. *Journal of Comparative Physiology B*, 167(2), 153–158.
- Rehorek, S., Legenzoff, E., Carmody, K., Smith, T., & Sedlmayr, J. (2005). Alligator tears: A reevaluation of the lacrimal apparatus of the crocodylians. *Journal of Morphology*, 266(3), 298–308.
- Rosenblatt, K.E., & Heithaus, M.R. (2011) Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *Journal of Animal Ecology* 80 : 786-798.
- Rozen-Rechels, D., Dupoué, A., Lourdais, O., Chamaillé-Jammes, S., Meylan, S., Clobert, J., & Le Galliard, J.F., 2019. When water interacts with temperature: Ecological and evolutionary implications of thermo-hydroregulation in terrestrial ectotherms. *Ecology and evolution*, 9(17), 10029–10043.
- Sannolo, M. & Carretero, M.A., 2019. Dehydration constrains thermoregulation and space use in lizards. *PLoS One*, 14(7), p.e0220384.
- Saunders, M. A., & Lea, A. S. (2005). Seasonal prediction of hurricane activity reaching the coast of the United States. *Nature*, 434(7036), 1005–1008.
- Schriever, T. A., Ramspott, J., Crother, B. I., & Fontenot, C. L. (2009). Effects of hurricanes Ivan, Katrina, and Rita on a southeastern Louisiana herpetofauna. *Wetlands*, 29(1), 112–122.
- Seebacher, F., Guderley, H., Elsey, R.M. and Trosclair III, P.L., 2003. Seasonal acclimatisation of muscle metabolic enzymes in a reptile (*Alligator mississippiensis*). *Journal of Experimental Biology*, 206(7), 1193–1200.
- Seebacher, F., Elsey, R.M. and Trosclair III, P.L., 2003. Body temperature null distributions in reptiles with nonzero heat capacity: Seasonal thermoregulation in the American alligator (*Alligator mississippiensis*). *Physiological and Biochemical Zoology*, 76(3), 348–359.
- Seebacher, F. (2005). A review of thermoregulation and physiological performance in reptiles: what is the role of phenotypic flexibility? *Journal of Comparative Physiology B*, 175(7), 453–461.
- Slip, D. J., & Shine, R. (1988). Thermophilic response to feeding of the diamond python, *Morelia s. spilota* (Serpentes: Boidae). *Comparative Biochemistry and Physiology--Part A: Physiology*, 89(4), 645–650.
- Strickland, B. A., Gastrich, K., Mazzotti, F. J., Massie, J. A., Paz, V., Viadero, N., Rehage, J. S., & Heithaus, M. R. (2020). Variation in movement behavior of alligators after a major hurricane. *Animal Biotelemetry*, 8(1), 1–10.
- Taplin, L. E. (1985). Sodium and water budgets of the fasted estuarine crocodile, *Crocodylus porosus*, in sea water. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 155(4), 501–513.
- Taplin, L. E. (1988). Osmoregulation in crocodylians. *Biological Reviews*, 63(3), 333–377.
- Taplin, L. E., Grigg, G. C., Harlow, P., Ellis, T. M., & Dunson, W. A. (1982). Lingual salt glands in *Crocodylus acutus* and *C. johnstoni* and their absence from *Alligator mississippiensis* and *Caiman crocodilus*. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 149(1), 43–47.
- Willmer, P., Stone, G., & Johnston, I. (2009). *Environmental Physiology of Animals*. John Wiley & Sons.
- Wood, C., & Harrington, G. A. (2015). Influence of seasonal variations in sea level on the salinity regime of a coastal groundwater-fed wetland. *Groundwater*, 53(1), 90–98.
- Woodward, A. R., Hines, T.C., Abercrombie, C. L., & Nichols, J. D. 1987. Survival of young American alligators on Florida lake. *Journal of Wildlife Management*. 51(4), 931–937.