

## Unprovoked Mouth Gaping Behavior in Extant Crocodylia

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**ABSTRACT.**—Unprovoked mouth gaping behavior is ubiquitous throughout 24 extant members of Crocodylia, yet information on gaping is limited. Proposed hypotheses for gaping include thermoregulation and the evaluation of potential environmental conditions. To determine temperature effects, we tracked head surface ( $T_{sh}$ ), body surface ( $T_{sb}$ ), and ambient ( $T_a$ ) temperatures with insolation utilization and positions. To evaluate potential environmental stimuli, we tested behavioral effects (i.e., open-eye frequency) and recorded conspecific presence, day and night events, and interaction with flies and fish. We included 24 extant species representatives, with detailed assessments of American Alligators (*Alligator mississippiensis*), *Crocodylus siamensis*, *Crocodylus intermedius*, *Crocodylus rhombifer*, and *Crocodylus halli*. Observations occurred during a range of  $T_a$  (3.89–32.22°C) with mean  $T_{sh}$  consistently higher than both  $T_{sb}$  and  $T_a$  across all crocodilians. Differences in  $T_{sh}$  and  $T_a$  were most pronounced with head in the sun. However, no significant differences in  $T_{sh}$  and  $T_{sb}$  were detected for *A. mississippiensis* and *Cr. siamensis*. Conversely, *Cr. halli*, *Cr. intermedius*, and *Cr. rhombifer* demonstrated statistically higher  $T_{sh}$ . Gaping with open eyes was more common, yet modeling suggested a relationship with closed eyes and temperature. Anecdotal observations indicated weather changes may elicit mouth gaping, and we report the second nocturnal mouth gaping observation (the first for three species). Overall, mixed results indicated unprovoked mouth gaping is a complex behavior, making it difficult to draw clear cause and effect relationships. Future research may benefit from a focus on natural history and quantitative behavioral studies.

Biologists have long assumed crocodilians utilized behavioral and physiological mechanisms, including mouth gaping, to regulate body temperature ( $T_b$ ) and head temperature ( $T_h$ ) by dissipating excess heat (Guggisberg, 1972; Smith, 1979; Steel, 1989; Huchzermeyer, 2003). Unprovoked mouth gaping (Fig. 1) occurs in both wild and captive animals. Unprovoked gaping occurs when crocodilians open their mouths without the presence of noticeable external stimuli. The gular fold also separates the oral cavity from the pharynx (Pooley and Gans, 1976). Unprovoked mouth gaping is similar in appearance to thermoregulatory/panting behavior of modern terrestrial lizards (Crawford, 1972; Seebacher, 1999; Tattersall et al., 2006). However, crocodilians are far removed from heliothermic Squamata, as fossilized Crocodylomorpha can be traced back to 180–200 million years ago (Guillette Jr. et al., 1997; Janke and Arnason, 1997; Ouchley, 2013), lending caution to broad generalizations across taxa.

Previous thermoregulatory studies of crocodilians focused on cloacal and internal  $T_b$  (Colbert et al., 1946; Hutton, 1987; Tattersall et al., 2006), with little emphasis on  $T_h$  regulation. Of the existing literature, the effectiveness of mouth gaping on  $T_h$  reduction is inconclusive, with large species-specific variation and contradictory results between in situ observations and controlled laboratory/field experiments, warranting the need for further exploration. Field observations reported implied mouth gaping was effective for  $T_h$  reduction in *Crocodylus johnstoni* (Johnson, 1973), and was effective for evaporative cooling of the oral mucosa in young and adult *Crocodylus niloticus* (Cott, 1961; Cloudsley-Thompson, 1969), but not necessarily in avoiding  $T_b$  heat stress in *Cr. niloticus* (Diefenbach, 1975). Additionally, mouth gaping was not effective for  $T_b$  reduction in *Caiman crocodilus* (Diefenbach, 1975) and had minimal effect on  $T_h$  reduction in *Alligator mississippiensis*

(Johnson et al., 1978). In *Crocodylus porosus*, mouth gaping had a significant effect on  $T_h$  reduction (Johnson, 1974) but not on  $T_b$  (Grigg and Seebacher, 1999). Controlled laboratory and field experiments contradicted Johnson et al., (1978) and concluded a reduction in  $T_h$  and suppressed  $T_h$  heat gain, yet minimal  $T_b$  reduction, in mouth gaping *A. mississippiensis* (Spotila et al., 1977; Terpin et al., 1979; Lang, 1987).

Literature regarding Crocodylia mouth gaping behavior is limited. Although many experts have postulated why crocodilians mouth gape, even during unfavorably cold weather conditions (Loveridge, 1984; Huchzermeyer, 2003), published data are minimal regarding the circumstances (e.g., when and where) this behavior takes place. Cott (1961) published observations of wild *Cr. niloticus* mouth gaping with a record of air or ambient temperature ( $T_a$ ) and body position relative to the sun, concluding a higher percentage of *Cr. niloticus* mouth gaped when exposed to direct sunlight compared to shade. Johnson (1974) found mouth gaping with head position in a shaded area had no effect on  $T_h$  reduction, whereas gaping with the head exposed to the sun reduced  $T_h$  in *Cr. porosus*.

Television documentaries (e.g., “Crocodiles: Here Be Dragons”; National Geographic, 1998) often attribute mouth gaping as analogous to sweating, wherein heat stress conditions induce evaporative cooling of the temperature reduction system (Wilke et al., 2007). Although crocodilian tongue epithelium can generate a constant and substantial evaporative cooling effect, it may not necessarily influence  $T_h$  reduction (Loveridge, 1984). Numerous hypotheses have been generated to explain mouth gaping behavior (Table 1) and contributing factors (Table 2).

The objectives of this paper are to expand upon the literature of unprovoked mouth gaping in extant Crocodylia, glean potential mechanisms for this behavior using an observational study design. To determine temperature effects, we tracked head surface temperature ( $T_{sh}$ ), body surface temperature ( $T_{sb}$ ),  $T_a$ , and insolation (body and head positions relative to sun or shade). To evaluate behavioral effects, we recorded weather,

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FIG. 1. Examples of unprovoked mouth gaping behavior in various crocodilians. (A) Slender-snouted *Gavialis gangeticus*, (B) *Crocodylus rhombifer* with full sun radiating head and tongue, (C) *Crocodylus siamensis* with head in sun but no sunlight radiating tongue, and (D) *Alligator mississippiensis* in direct sunlight but no sunlight radiating tongue.

eyes open or shut, and environmental conditions for potential stimuli (e.g., interaction with fish and flies, night monitoring, individual vs. communal enclosures). We expected distinct relationships between  $T_{sh}$ ,  $T_{sb}$ , and  $T_a$ , with significant differ-

ences in  $T_{sh}$  and  $T_{sb}$  and associations with upper ranges of optimum  $T_a$ 's. Additionally, we expected to see gaping associated with head and body positioned in the sun and consistency between stimuli during gaping events.

TABLE 1. Compilation of published observations and hypotheses pertaining to both provoked and unprovoked mouth gaping behavior in reptiles.

Potential advantage	Source
Thermoregulation via $T_h$ reduction	Cott, 1961; Guggisberg, 1972; Johnson, 1974; Spotila et al., 1977; Terpin et al., 1979; Ouchley, 2013
Drying and killing ectoparasites (leeches)	Diefenbach, 1975; Johnson et al., 1978
Threatening/agonistic behavior toward noncrocodilians	Neill, 1971; Kofron, 1993; Brien et al., 2013
Lure flies for consumption	Neill, 1971
Warming	Huchzermeyer, 2003
Dominance behavior toward conspecific	Garrick and Lang, 1977; Thorbjarnarson and Hernández, 1993; Ray and Walley, 2003
Invitation for birds to eat decaying meat/leeches	Guggisberg, 1972
Increased sensitivity to airborne gustatory particles	Kofron, 1993

TABLE 2. Published list of factors and motivators that influence provoked and unprovoked mouth gaping behavior in reptiles.

Factors influencing mouth gaping	Source
Ontogenetic size	Modha, 1968; Seebacher, 1999; Harlow et al., 2010
Thermophilic response to last meal consumed	Lang, 1979; Grigg and Gans, 1992; Verdade et al., 1994
Seasonality	McIlhenny, 1935; Joenen and McNease, 1972; Grigg et al., 1998; Bassetti et al., 2014
Social behavior (crowding)	Loveridge, 1984; Lovich, 1990
Relative humidity/circulation of air around the mouth (similar to panting in mammals)	Diefenbach, 1975
Insolation	Cott, 1961; Guggisberg, 1972
Gigantothermy (ectothermic homeothermy)	Colbert et al., 1946; Grigg et al., 1998
Species-specific: crocodiles more than alligators	Scott, 2004

## MATERIALS AND METHODS

**Study Location and Animals.**—We conducted this study from August 2017 to January 2018 at the St. Augustine Alligator Farm Zoological Park (SAAFZP), Florida, USA. The SAAFZP displayed over 600 individual crocodilians representing 24 extant species (Table 3). This study only included captive crocodilians, which is advantageous as captive specimens display a higher tolerance toward conspecifics and are therefore less likely to express agonistic behavior (Lang, 1987). The monitored crocodilians were typically isolated from conspecifics or paired with a respective mate or several potential mates, with the exception of *A. mississippiensis* housed communally and separated by size (juveniles, subadults, and adults) and *Crocodylus siamensis* housed communally (juveniles and adults). All 24 extant species were not equally represented in number of individuals, age, or sex. This study excluded hatchling and neonate crocodilians (<1 yr) to avoid discrepancy in determining provoked vs. unprovoked mouth gaping observations, as newborn crocodilians are hard wired from birth to display greater agonistic behavior than adults (Brien et al., 2013). We recorded data for adult, subadult, and juvenile crocodilians. The five species with the highest frequency of mouth gaping observations varied in total number of

individuals available for the study, being *A. mississippiensis*, *Cr. siamensis*, *Crocodylus intermedius*, *Crocodylus rhombifer*, and *Crocodylus halli* (= *Crocodylus novaeguineae*; Murray et al., 2019) (Table 3). All monitored crocodilians were adults except *Cr. siamensis* (6 adults, 30 juveniles), *Cr. halli* (1 adult, 2 subadults), *Mecistops cataphractus* (6 adults, 4 subadults, 4 juveniles), *Crocodylus palustris* (1 adult, 2 juveniles), and an indeterminate number of *A. mississippiensis* (~150 adults, ~50 subadults, >150 unknowns).

**Habitats.**—Climate conditions of St. Augustine, Florida were humid subtropical, with average  $T_a$  between 20–32°C. All crocodilians were housed outdoors with groundwater wells supplying continuous running water pools maintaining temperature between 20–22°C.

**Observations.**—We conducted the study ad libitum (i.e., not set to strict time restraints or specific enclosures) observing all 24 species at least twice a day, 5 d a week. Similar to previous event-based observational studies, in which duration of behavior was not recorded (Augustine et al., 2017), this examination took a systematic observational approach (Bakeman and Gottman, 1997). Metrics recorded were as follows: species, individual, date, time of day, enclosure number, sex, size (adult, subadult, juvenile),  $T_a$ ,  $T_{sb}$ ,  $T_{sh}$ , eyes open or closed, weather conditions (sunny, overcast, raining), and insolation position (body com-

TABLE 3. List of all crocodilians studied with number of individuals ( $n$ ), highest ambient temperature ( $T_a$ ), and lowest  $T_a$  for each species observed mouth gaping, current geographic range, and International Union for Conservation of Nature (IUCN, 2020) conservation status of least concern (LC), vulnerable (VU), critically endangered (CR), conservation dependent (CD), and not evaluated (NE).

Species	$n$	Lowest $T_a$ °C	Highest $T_a$ °C	Geographic range	Status
<i>Alligator mississippiensis</i>	>350	6.7	29.4	Southeast United States	LC
<i>Alligator sinensis</i>	9	16.1	28.9	East China	CR
<i>Caiman crocodilus</i>	6	21.7	26.7	Central and South America	LC
<i>Caiman yacare</i>	2			South America	LC
<i>Paleosuchus palpebrosus</i>	4	17.2	29.4	South America	LC
<i>Paleosuchus trigonatus</i>	12	27.2	29.4	South America	LC
<i>Caiman latirostris</i>	10	6.1	28.3	South America	LC
<i>Melanosuchus niger</i>	2	23.3	25.6	South America	CD
<i>Crocodylus acutus</i>	2			North, Central, and South America	VU
<i>Crocodylus moreletii</i>	1	6.1	32.2	Central America	LC
<i>Crocodylus rhombifer</i>	4	6.1	32.2	Cuba	CR
<i>Crocodylus intermedius</i>	5	3.9	32.2	South America	CR
<i>Crocodylus suchus</i>	4	3.9	32.2	Africa	NE
<i>Crocodylus niloticus</i>	5	18.3	18.3	Africa	LC
<i>Crocodylus palustris</i>	3	6.1	28.9	South Asia	VU
<i>Crocodylus porosus</i>	2	6.1	30.0	Australasia and South Asia	LC
<i>Crocodylus mindorensis</i>	2	16.7	28.9	Philippines	CR
<i>Crocodylus siamensis</i>	36	3.9	32.2	Southeast Asia	CR
<i>Crocodylus johnstoni</i>	3	11.7	30.0	Australia	LC
<i>Crocodylus halli</i>	3	14.4	32.2	South New Guinea	NE
<i>Mecistops cataphractus</i>	11	6.1	31.1	Africa	CR
<i>Osteolaemus tetraspis</i>	6	23.3	31.1	Africa	VU
<i>Tomistoma schlegelii</i>	4	21.7	29.4	Southeast Asia	VU
<i>Gavialis gangeticus</i>	3	18.9	32.2	South Asia	CR



pletely/partially/not in sun, head in sun/shade). We opportunistically documented any potential external stimuli during mouth gaping events, including interactions with other organisms and simultaneous gaping with environmental changes. Such opportunistic mouth gaping events can be useful for further testing.

Several factors constrained this study to omit observations made in the spring and early summer months of the year (February–July). First, increased bellowing is more frequent during the courting season (February–May at the SAAFZP) and is typically understood to be a sexual attractant (Carr, 1967; Garrick and Lang, 1977) or agonistic behavior to conspecifics (Kellogg, 1929; Oliver, 1955; Vliet, 1989). Mistaking an agonistic mouth gaping event for one unprovoked would have been likely. Second,  $T_b$  in female *Caiman latirostris*, and presumably all crocodilians, can vary in relation to reproductive condition, including seasonality (Bassetti et al., 2014). Vitellogenesis (i.e., yolk production in the oocyte) and oogenesis occur in the spring and extend into midsummer (May–July at the SAAFZP) as  $T_a$  increases (Joanen and McNease, 1980, 1989; Lance, 1989; Guillette et al., 1997), except for SAAFZP *Cr. johnstoni* and *Gavialis gangeticus*, which typically deposited eggs in March, SAAFZP *Cr. intermedius*, which sometimes exhibited courting behavior in October and November, and American Crocodiles (*Crocodylus acutus*), which have bred in January and February (Kushlan and Mazzotti, 1989). And third, aggressive interactions during the courting/nesting season can affect  $T_b$  in displaced subordinate crocodilians from normal basking areas (Seebacher and Grigg, 1997; Seebacher et al., 1999).

We used a Raytek MT6 Infrared Thermometer “Thermo gun” (Raytek, Santa Cruz, California, USA) equipped with a 1 : 10 heat-source diameter-to-distance ratio to record  $T_{sb}$ , centered midway down the osteoderm columns at a 90° angle, and  $T_{sh}$ , centered on the cranial table at a 90° angle. We did not record  $T_{sh}$  and  $T_{sb}$  on individuals at a distance >1.8 m because of potential inaccuracy, especially regarding posterior width of the cranial table that can be <18 cm in 2.7 m snout–vent length (SVL) crocodilians (Hall and Portier, 1994). We did not obtain  $T_{sh}$  on crocodilians <2.7 m SVL unless we could safely procure temperature readings <1.8 m from the cranial table. We obtained  $T_a$  at the time of the mouth gaping observation from a nearby weather station (KFLSTAUG19 at 29.894490°N, –81.296396°W, datum WGS 84), controlled by a Davis Vantage Vue monitoring station (Davis Instruments, Hayward, California, USA) utilizing MétéoBridge software (version 1.x, Lentföhrden, Germany).

**Survey.**—We distributed an electronic mail survey to 390 zookeepers and crocodilian biologists asking two questions based on their expertise: 1) What factors contribute to unprovoked mouth gaping in crocodilians?; and 2) What are potential advantages of unprovoked mouth gaping in crocodilians? This survey was sent out on 23 April 2018 and left open for a collection period of 30 d.

**Statistical Analysis.**—This study employed statistical analyses using the open-source statistics software “R” (R Core Team, 2014). In addition to summary statistics, nonparametric tests were applied as data failed to meet assumptions of normality and homoscedasticity, regardless of transformations. A series of Wilcoxon Signed Rank Tests (nonparametric paired  $t$ -test) were performed to detect differences between  $T_a$  and  $T_{sb}$ ,  $T_a$  and  $T_{sh}$ , as well as  $T_{sb}$  and  $T_{sh}$  ( $\alpha = 0.05$ ). False Discovery Rate (FDR) adjustments (Benjamini and Hochberg, 1995) were applied to  $t$ -test values following Dalmasso et al. (2005). Analyses included

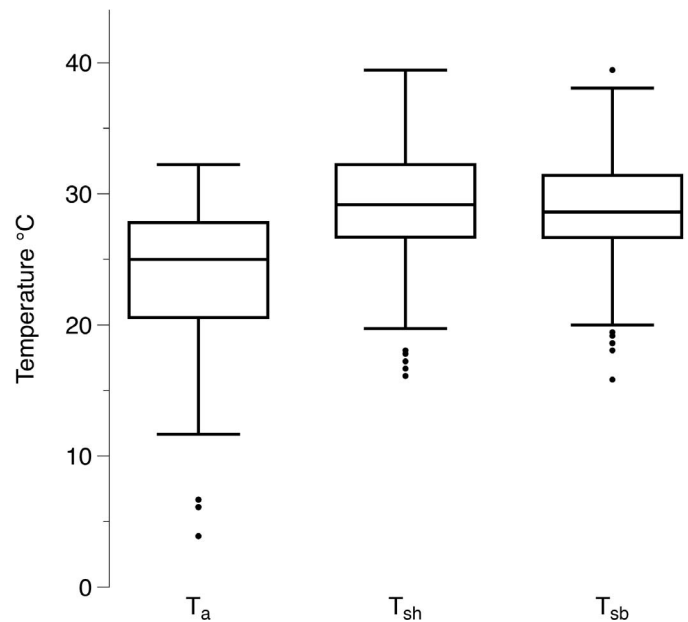


FIG. 2. Temperature ranges for ambient ( $T_a$ ) surface head ( $T_{sh}$ ), and surface body ( $T_{sb}$ ) across all crocodilians collectively. Values for box and whiskers represent observations across all species. Lines represent Interquartile Range with means and outliers.

pooled data comprising all species in addition to comparisons of species-specific differences for the top five by number of observations ( $n$ ): *Cr. siamensis* ( $n = 109$ ), *Cr. rhombifer* ( $n = 85$ ), *Cr. intermedius* ( $n = 71$ ), *A. mississippiensis* ( $n = 57$ ), and *Cr. halli* ( $n = 48$ ); while observations for each individual were paired for  $T_a$ ,  $T_{sb}$ , and  $T_{sh}$ .

Linear mixed effects models were constructed using the R package *lme4* (Bates et al., 2015) to evaluate the effects of  $T_a$  and  $T_{sb}$  on  $T_{sh}$  using a repeated measures design. The models included  $T_a$  and  $T_{sb}$  as fixed effects, with species and individual as random effects:  $T_{sh} \sim T_a + T_{sb} + (1|species) + (1|individual)$ . Models were also constructed to evaluate the relationships between the magnitude of temperature differences ( $T_d$ ) between  $T_{sh}$  and  $T_a$  considering eye position (open or closed), head position (sun or shade), body position (sun or shade), sex, weather (sunny, overcast, rain) and  $T_a$ 's. Fixed effects included eyes (E), head position (H), body position (B), sex (S), and weather (W) with species and individual random effects:  $T_d \sim E + H + B + S + W + (1|species) + (1|individual)$ . Models were selected based on QQ plots of residuals and Bayesian Information Criterion (BIC) values and  $P$ -values following Maximum Likelihood Ratio (LRT) testing.

## RESULTS

Twenty-two crocodilian species displayed unprovoked mouth gaping at least once. Although included in the study, *Cr. acutus* and *Caiman yacare* were never observed mouth gaping. The highest frequency of observed mouth gaping events occurred with *Cr. siamensis* ( $n = 109$ ) and the lowest frequency with *Melanosuchus niger* ( $n = 3$ ).

**Temperature Results.**—Across all crocodilians collectively, paired Wilcoxon Signed Rank Tests (WSRT) indicated median  $T_{sh}$  were not significantly higher than  $T_{sb}$  while mouth gaping ( $Z = 0.299$ ,  $P = 0.1815$ ; Fig. 2). Nonparametric  $t$ -tests on species-specific patterns revealed *Cr. halli*, *Cr. intermedius*, and *Cr. rhombifer* demonstrated statistically higher  $T_{sh}$ , while no significant

TABLE 4. Temperature range, mean, standard deviation (SD), and Wilcoxon Signed Rank Test statistical analysis for surface body ( $T_{sb}$ ), surface head ( $T_{sh}$ ), and ambient ( $T_a$ ) temperature in five species with the highest frequency of mouth gaping observations. Sex ratio of males (M) to females (F) and eye frequency data reported for each species.

Species ( <i>n</i> = individual observations)	( $T_{sb}$ Range) Mean $T_{sb} \pm SD^\circ C$ ( <i>n</i> )	( $T_a$ Range) Mean $T_a \pm SD^\circ C$ ( <i>n</i> )	( $T_a$ Range) Mean $T_a \pm SD^\circ C$ ( <i>n</i> )	Sex ratio M : F	$T_{sh}$ and $T_{sb}$ Z-value, df	$T_{sh}$ and $T_a$ Z-value, df	$T_{sb}$ and $T_a$ Z-value, df	Eyes open (O) and closed (C) ( <i>n</i> )
<i>Crocodylus intermedius</i> (71)	(18.6–39.4) 28.3 $\pm$ 4.3 (48)	(21.9–37.5) 28.9 $\pm$ 4.1 (45)	(3.9–32.2) 24.4 $\pm$ 9.8 (45)	20 : 51	Z = 0.616, P = 0.03, 44	Z = 1.299, P < 0.0001, 44	Z = 1.241, P < 0.0001, 44	O: 85.9% C: 14.1% (65)
<i>Crocodylus halli</i> (48)	(18–37.8) 28.1 $\pm$ 4 (42)	(17.2–35) 28.6 $\pm$ 3.6 (41)	(14.4–32.2) 24.4 $\pm$ 8.6 (41)	48 : 0	Z = 0.490, P = 0.047, 40	Z = 1.123, P < 0.0001, 40	Z = 1.030, P < 0.0001, 40	O: 84.6% C: 15.4% (37)
<i>Alligator mississippiensis</i> (57)	(15.8–35.3) 28.8 $\pm$ 4.5 (24)	(16.7–36.7) 28.8 $\pm$ 4.7 (24)	(6.7–29.4) 23.5 $\pm$ 11.4 (24)	20 : 4	Z = 0.041, P = 0.856, 23	Z = 0.955, P < 0.0001, 23	Z = 0.990, P < 0.0001, 23	O: 72.7% C: 27.3% (44)
<i>Crocodylus rhombifer</i> (85)	(20.3–35.8) 29.1 $\pm$ 3.2 (79)	(14.7–36.4) 29.5 $\pm$ 3.5 (80)	(6.1–32.2) 23.7 $\pm$ 8.7 (80)	31 : 54	Z = 0.546, P = 0.038, 79	Z = 1.748, P < 0.0001, 24	Z = 1.736, P < 0.0001, 24	O: 95.3% C: 4.7% (77)
<i>Crocodylus siamensis</i> (109)	(21.4–35) 29.3 $\pm$ 3.3 (49)	(21.1–34.4) 29 $\pm$ 3.2 (48)	(3.9–32.2) 23.3 $\pm$ 10.8 (48)	34 : 26	Z = 0.384, P = 0.108, 48	Z = 1.264, P < 0.0001, 25	Z = 1.345, P < 0.0001, 25	O: 88% C: 12% (99)

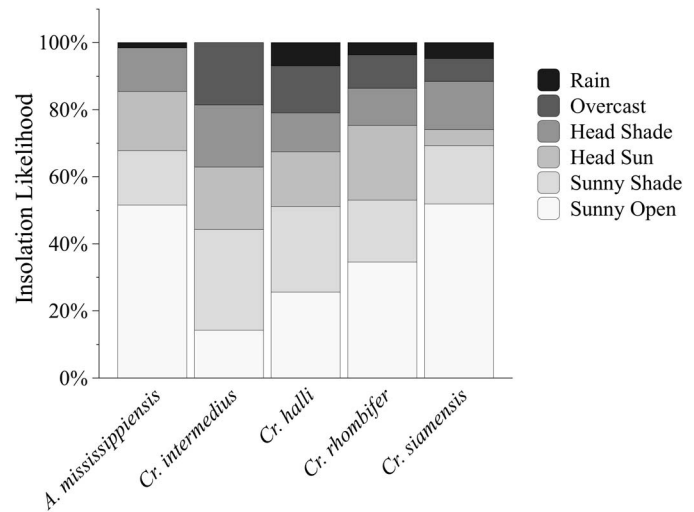


FIG. 3. Visual representation of insolation frequency in selected species. “Rain” = overcast and raining weather conditions. “Overcast” = complete cloud cover. “Head Shade” = sunny weather but head was in a shaded area. “Head Sun” = sunny weather and head in direct sunlight. “Sunny Shade” = sunny weather but both crocodilian body and head in shaded area. “Sunny Open” = sunny weather and both crocodilian body and head in direct sunlight.

differences in  $T_{sh}$  and  $T_{sb}$  were detected for *A. mississippiensis* and *Cr. siamensis* (Table 4).

Median  $T_{sb}$  and median  $T_{sh}$  were both significantly higher than  $T_a$  across all crocodilians in all weather conditions (paired one-sided WSRT:  $T_{sh}$ ,  $Z = 3.527$ ,  $P < 0.0001$ ;  $T_{sb}$ ,  $Z = 3.507$ ,  $P < 0.001$ ) and held true for each of the five selected crocodilian species (Table 4). Median  $T_{sh}$  and median  $T_{sb}$  were significantly different from  $T_a$  across 39 mouth gaping observations in overcast/raining conditions or at night (paired two-sided WSRT:  $T_{sh}$ ,  $Z = 1.052$ ,  $P < 0.0001$ ;  $T_{sb}$ ,  $Z = 1.014$ ,  $P < 0.0001$ ). The mean  $T_a$  for all mouth gaping occurrences was  $23.8^\circ C$  ( $n = 370$ ) while minimum and maximum observations for  $T_a$  were  $3.9^\circ C$  and  $32.2^\circ C$  (Table 3).

Across all species (values represent means  $\pm$  SE),  $T_{sh}$  of  $29.2^\circ C$  ( $\pm 0.01$ ) was consistently higher than  $T_{sb}$  and  $T_a$  of  $28.9^\circ C$  ( $\pm 0.01$ ) and  $23.8^\circ C$  ( $\pm 0.01$ ). Variation in  $T_{sh}$  is best explained by  $T_{sb}$ , as  $T_{sh}$  increases by  $0.8^\circ C$  relative to  $T_{sb}$ , but only by  $0.1^\circ C$  for  $T_a$  (LMM fit with LRT:  $\chi^2 = 48.4$ ,  $P < 0.001$  and  $\chi^2 = 14.9$ ,  $P < 0.001$  for  $T_{sb}$  and  $T_a$ , respectively).

**Insolation, Weather Condition, Eye, and Size Results.**—Crocodilian insolation posturing on sunny days varied greatly between the five selected species, with fully exposed (both head and body) as low as 14.7% in *Cr. intermedius* and as high as 52.9% in *Cr. siamensis*. The five selected species exhibited varied body position results during mouth gaping activity in different weather conditions (Fig. 3). The closed-eye occurrence frequency while mouth gaping was 13% across all crocodilians ( $n = 491$ ). Size classes were not equally represented because of the opportunistic study design; however, adult *Cr. siamensis* in this study mouth gaped more often (87.16%) than did juvenile *Cr. siamensis* (12.84%).

Across species,  $T_d$  between  $T_{sh}$  and  $T_a$  averaged  $5.4^\circ C$  ( $\pm 0.01$  SE). Eye position (open or closed) was a significant predictor for  $T_d$ , as closed eyes reflect a temperature increase of  $1.9^\circ C$  relative to eyes open (LMM fit with LRT,  $\chi^2 = 28.7$ ,  $P < 0.001$ ). Head and body position were also significant predictors, with head in the sun yielding an increase of  $4.5^\circ C$  compared to the shade and body in the sun yielding an increase of  $1.6^\circ C$  compared to



FIG. 4. Multiple flies were seen on the lingual oral mucosa and tongue of this mouth gaping *Alligator mississippiensis*, contradicting the claim crocodilians will mouth gape to consume flies.



FIG. 5. Male *Crocodylus porosus* mouth gaping underwater. Although no fish are in this enclosure, small cleaner fish have been documented to pick at the teeth of submerged *Crocodylus acutus* and *Alligator mississippiensis*.

shade (LMM fit with LRT,  $\chi^2 = 28.8$ ,  $P < 0.001$  and  $\chi^2 = 13.1$ ,  $P < 0.001$  for head and body position, respectively). Interestingly, sex was not a significant factor and was removed from the model (LMM fit with LRT:  $\chi^2 = 3.2$ ,  $P = 0.2$ ). Conversely, weather was a significant variable, most notably between sun and rain with a decrease of 6.2°C followed by sun to overcast decreasing by 4.6°C (LMM fit with LRT:  $\chi^2 = 38.8$ ,  $P < 0.001$ ).

**Opportunistic Behavioral Results.**—A single *Cr. palustris* (#91284) accounted for a disproportional amount of observations, with 4.28% of the total ( $n = 561$ ), whereas two *Cr. acutus* and two *C. yacare* accounted for 0.00% of the total. On multiple occasions, crocodilians showed no behavioral response to flies landing on their tongues (Fig. 4), and one individual adult *Cr. porosus* (#A03162) frequently gaped underwater in the absence of fish (Fig. 5). An anecdotal example of weather/excitatory events coinciding with a behavioral response occurred after Hurricane Irma hit the SAAFZP. On 12 September 2017, after the storm passed and weather conditions were sunny with  $T_a = 28.9^\circ\text{C}$ , staff filled the half-empty pools back to their original levels. Concurrent with filling the main Alligator Lagoon pool (which housed 36 *A. mississippiensis*), nearly every individual began bellowing, which is seldom observed outside of spring. We observed many *A. mississippiensis* exiting the pool once filled at ~1320 h, and >18 specimens maintained long-term mouth gaping over the course of a few hours. We additionally observed mouth gaping on a fair-weather night after 2000 h with  $T_a = 26.1^\circ\text{C}$  on 18 September 2017. Observations included an adult female *Crocodylus mindorensis*, adult male *Cr. halli* ( $T_{sb}$ : 28.6°C;  $T_{sh}$ :

28.9°C), subadult male *Cr. halli* ( $T_{sb}$ : 25.8°C;  $T_{sh}$ : 25.8°C), and an adult male *Cr. siamensis* ( $T_{sb}$ : 30.3°C;  $T_{sh}$ : 29.7°C).

**Survey Results.**—We received 18 responses for a response rate of 5% from the electronic questionnaire. A range of answers that have not been published in previous literature included: facilitated breathing (during high relative humidity or with respiratory illness), improved low-frequency auditory ability, dental health, relaxation (especially regarding muscle-relaxing drugs), and inattentive behavior (Table 5). Responses that coincided with published literature were not included in this study.

DISCUSSION

Temperature effects are sometimes suggested to explain unprovoked mouth gaping behavior in crocodilians, whether to alleviate heat stress (Wilke et al., 2007) or moderate temperature differences between tissues (Loveridge, 1984). Although our observations cannot dismiss gaping affecting temperature, we suggest mouth gaping is a complex behavior that may also be motivated by other behavioral cues.

**Temperature and Mouth Gaping.**—Two crocodilian species did not exhibit significantly higher  $T_{sh}$  than  $T_{sb}$  (Table 4). Johnson (1974) also observed no differences between  $T_b$  and  $T_h$  in artificially heated and thermocoupled *Cr. novaeguineae* and *Cr. porosus*. The magnitude of difference ( $T_d$ ) between  $T_{sh}$  and  $T_a$  was mainly a function of head position (4.5°C difference between sun

TABLE 5. List of unpublished potential advantages of unprovoked mouth gaping behavior from an electronic mail questionnaire.

Potential advantage	Source
Facilitated breathing during high relative humidity	Sidney Godfrey (Biologist; University of Florida: Institute of Food and Agricultural Sciences)
Improved low-frequency auditory ability	Vladimir Dinets (Zoologist; Okinawa Institute of Science and Technology)
Dental health	Vladimir Dinets (Zoologist; Okinawa Institute of Science and Technology)
Easier to breathe when sick with respiratory illness	Mark Beshel (Assistant Curator of Living Collections; National Mississippi River Museum and Aquarium)
Relaxation, especially regarding muscle relaxing drugs	Romulus Whitaker (Herpetologist; Madras Crocodile Bank)
Inattentive behavior	John Brueggen (General Director; SAAFZP)

and shade) rather than body position (1.6°C between sun and shade).

Interestingly, gaping *A. mississippiensis*  $T_{sb}$ ,  $T_{sh}$ , and  $T_a$  (Table 4) were below the preferred optimum  $T_b$  (33.4–35°C) (Colbert et al., 1946; Johnson, 1974; Lang, 1979). This is somewhat surprising, as thermoregulatory studies indicate skin temperature is typically higher than core  $T_b$  in reptiles (Andrews, 2008; Carretero, 2012; Halliday and Blouin-Demers, 2017). Conversely,  $T_{sb}$ 's and  $T_{sh}$ 's of the four crocodile species (Table 4) were within the preferred optimal  $T_b$  (28–32°C) for both captive and wild hatchling *Cr. acutus* (Lang, 1975, 1979) and the maximum mean  $T_b$  (26.9–29.2°C) for *Cr. niloticus* (Downs et al., 2008).

Mouth gaping can be effective for cooling areas of the body (Cloudsley-Thompson, 1969; Spotila et al., 1977; Terpin et al., 1979; Lang, 1987). However, nonuniform insolation positions (Fig. 3) indicated crocodilians do not mouth gape exclusively to cool off. Huchzermeyer (2003) suggested sunlight radiation on the interior buccal surface area (see Fig. 1B) facilitated potential  $T_h$  and  $T_b$  elevation. Yet, shadow cast from the maxilla often interfered with this potential (e.g., Fig. 1C,D), and the small surface area of slender-snouted Crocodylia (e.g., Fig. 1A) also limited this effect. Solar radiation is unnecessary to increase  $T_b$  via mouth gaping, provided  $T_a > T_b$  and high relative humidity (Diefenbach, 1975). Further research is needed in a controlled setting to decouple these relationships. However, the diversity of insolation observations in the current study (Fig. 3) is consistent with wild *Cr. johnstoni*, which employ an array of behavioral postures to maintain operative temperatures (Seebacher, 1999).

We were unable to adequately test for size as a factor because of the limited number of size classes with few observations for juveniles. A more pronounced surface area-to-bulk ratio of larger animals provides a greater capacity for heat storage (Cott, 1961; Grigg and Gans, 1992), which may explain why, if larger crocodilians require a longer time to internally reach optimal  $T_b$ , adult *Cr. siamensis* mouth gaped more often than their juvenile counterparts.

We report surface temperatures and not core  $T_b$ , lending caution when interpreting results. For example, skin temperature is typically higher than cloaca temperature in warming Common Gartersnakes (*Thamnophis sirtalis*) (Halliday and Blouin-Demers, 2017) and lizards (Andrews, 2008; Carretero, 2012). However,  $T_b$  and  $T_h$  studies are invasive and can alter behaviors, requiring some experiments to stimulate gaping by propping the mouth open (Spotila et al., 1977). Core  $T_b$  requires researchers to surgically implant dataloggers/thermocouples (Johnson, 1974; Glanville and Seebacher, 2006; Downs et al., 2008; Bassetti et al., 2014), administer them orally as pseudo-gastroliths (Loveridge, 1984; Grigg et al., 1998), or perform cloaca probing (Cott, 1961; Brisbin et al., 1982; Loveridge, 1984; Hutton, 1987). Conversely, we utilized a Thermo gun so natural behaviors would not be compromised from handling stress following cloaca capsule insertion or datalogger attachment. Additionally, SAAFZP crocodilians were accustomed to daily human presence and were typically <1.8 m from the Thermo gun, allowing for accuracy beyond that of a wild scenario. We also acknowledge that while  $T_a$  and direct solar radiation influence crocodilian thermoregulation, heat from the ground may also radiate via conduction, which would alter individual behavior (Bassetti et al., 2014). Additionally, effects of wind and solar conductance can affect the true thermal condition (i.e.,  $T_a$ ) for each mouth gaping event (Chappell, 1981).

**Behavioral Factors Influencing Mouth Gaping.**—The literature contains many hypotheses for mouth gaping (Table 1) in addition to unpublished ones that include behavioral responses and physiological benefits (Table 5). Individual behavior/traits may factor into gaping. Although we did not document *Cr. acutus* or *C. yacare* mouth gape, *Cr. acutus* have mouth gaped in captivity and in the wild (Gamble, crocodilian trainer; Lloret, crocodilian biologist, pers. comm.), whereas *C. yacare* have mouth gaped in captivity (Gamble, pers. comm.). Loveridge (1984) noted that monitoring individual behavior, similar to the present study, could be more informative than following large groups of crocodilians, as individual personality differences may yield variability in gaping behavior.

Dominance behavior is plausible, although many crocodilians were isolated (e.g., all four *Cr. rhombifer* were isolated from conspecifics). Our models did not detect a relationship between sex and gaping behavior. Sleeping and inattentive behavior is also unlikely as results show a low ratio of closed-eye occurrences (13% [ $n = 491$ ]; Table 4). Yet across species, modeling indicated gaping with closed eyes reflected elevated  $T_d$  by 2°C. Both head and body position were important factors explaining differences between  $T_{sh}$  and  $T_a$  while gaping; however, head position exerted a stronger influence. Insolation appears to play a role in the behavior, although limitations of this study did not determine exact mechanisms. Therefore, we were unable to detangle behavioral and thermoregulatory responses and warrants further study.

There is documentation of fish 'cleaning' the teeth of submerged *Cr. acutus* (Guggisberg, 1972; Dinets, 2013a) and *A. mississippiensis* mouths (Darlington, reptile curator, pers. comm.). Our opportunistic observations of crocodilian interactions with other organisms suggest a potential relationship between crocodilians and fish/flyes. If such an association exists with cleaner fish, it is interesting that the submerged *Cr. porosus* (#A03162) mouth gaped in the absence of fish.

**Additional Factors Influencing Mouth Gaping.**—Weather may play a larger role than previous studies have indicated. We detected a significant relationship between  $T_d$  and weather, with substantial temperature differences between sun and rain. A sudden weather change can elicit mouth gaping, as indicated by behavioral responses in *Cr. niloticus* with respect to localized weather (Loveridge, 1984), seasonal weather, and behavior in *A. mississippiensis* (Brisbin et al., 1982) and posturing/movement in relation to weather by *Cr. johnstoni* (Seebacher and Grigg, 1997). Wild *Cr. niloticus* mouth gaped immediately after exiting water (Loveridge, 1984), similar to our documentation of >18 *A. mississippiensis* maintaining long-term gaping after exiting the pool following several days of reduced water. Curiously, we rarely recorded these 36 individuals gaping otherwise. This suggests excitatory events may produce changes in behavior such as gaping and vocalizations typically only heard during breeding season.

We report the second published nocturnal mouth gaping observation and the first for three species (i.e., *Cr. mindorensis*, *Cr. halli*, and *Cr. siamensis*). Loveridge (1984) observed nocturnal mouth gaping in a single *Cr. niloticus*. Dinets (2010) documented nocturnal stationary terrestrial behavior (lying on land) in five species of wild crocodilians, with no overlap of the aforementioned three species we observed. We did not note any probable stimuli to elicit these occurrences.

**Recommendations for Future Research.**—Future research should consider factors of mouth gaping behavior in crocodilians beyond thermoregulation (Table 5). The range of environmental

conditions and insolation likelihood rendered in this study, in addition to that of the literature, indicated gaping behavior is complex, making it difficult to draw clear cause and effect relationships. Future studies may benefit from a focus on natural history and behavior, as  $T_a$  and insolation likelihood fail to significantly factor into mouth gaping. This may reveal communication patterns associated with mouth gaping, as crocodilians are arguably the most behaviorally complex extant reptiles (Thorbjarnarson and Hernández, 1993). Long distance signaling is conserved across Crocodylia phylogenetic families (Dinets, 2013b), increasing the likelihood that gaping is a form of social behavior/communication.

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