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Activity Budget and Behavioral Patterns of American Crocodiles (*Crocodylus acutus*) in Belize

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Abstract.—**American Crocodiles (*Crocodylus acutus*) are broadly distributed throughout coastal and low-elevation tropical wetlands in the Americas and Caribbean. Despite years of ecological research on this species, there is still a dearth of behavioral data on wild American Crocodiles. Our project established diurnal time-activity budgets for American Crocodiles in Belize and evaluated behavioral patterns in relation to season (wet and dry) and time of observation (morning and afternoon). Crocodiles are dynamic and alter activity budgets in response to seasonal, temporal, and climatic changes, thus the use of time-activity budgets can be significant for documenting behavioral patterns, and a tool to quantify bioenergetic investment. We collected behavioral observations of wild crocodiles from multiple sites in Belize from May 2015 to August 2017. American Crocodiles allotted the greatest amount of time performing maintenance activities, including basking and floating on the surface of the water with head or body exposed. We found time allotment for other behaviors, particularly agonistic and social displays, were proportionally greater during the dry season in conjunction with the breeding season. Overall, our research creates a current baseline from which further studies could investigate changes in activity budgets in relation to mounting threats from climate change and anthropogenic activity.**

Key Words.—conservation; crocodylian; ecology; Mesoamerica; time-activity budget

Introduction

Wildlife are impacted by their environment, and documentation of behaviors can serve as a metric for understanding interactions between wildlife and their respective ecosystems (Manning and Dawkins 1998; Dwyer 2004; Sumpter 2010). Increasingly, climate change and anthropogenic activity are factors that shape wildlife behavior (Griffiths and Van Schaik 1993; Luniak 2004; Blickley and Patricelli 2010; Hovick et al. 2014). Alteration of wildlife behavior can have deleterious effects on the biology and ecology of affected populations (Laiolo 2010). Crocodylians are resilient predators that have persisted through extensive environmental changes and global cataclysmic events (Roos et al. 2007). Extensive research on a few species of crocodylians suggests some species and/or populations serve as ecosystem engineers and apex predators in their respective habitats (Nifong and Silliman 2013; Somaweera et al. 2019). Despite their potential importance within ecosystems, there is still a lack of data regarding crocodylian behavior (Thorbjarnarson 1989).

American Crocodiles (*Crocodylus acutus*) have the widest distribution of the New World crocodylians. They range from the southern tip of Florida, USA, to northern South America along the Atlantic coast, and occur in suitable habitat along the Pacific coast from southern Mexico to Ecuador, in addition to inhabiting various Caribbean islands (Ernst et al. 1999). In the mid-1900s, intense, unregulated exploitation for commercial harvest nearly extirpated this species in areas throughout its range (Thorbjarnarson 1989; Thorbjarnarson et al. 2006). Protection implemented through international and national laws in the early 1970s assisted in facilitating the recovery of some American Crocodile populations, generating its status as Vulnerable by the International Union for the Conservation of Nature (IUCN; 2012). Belize, a small Central American country located south of Mexico on the Caribbean coast, experienced dramatic population declines of American Crocodiles during the aforementioned period of overexploitation. Currently, American Crocodile populations in Belize, particularly on offshore islands have recovered somewhat, while mainland populations remain low and data for these populations are deficient (Platt and Thorbjarnarson 2000a). Although commercial hunting has ceased, pollution and habitat destruction have emerged as significant threats to current crocodile populations (Platt and Thorbjarnarson 2000a; Tellez et al. 2016). As tourism and coastal development continues to expand, and environmental risks to coastal ecosystems mount with climate change, it is reasonable to predict such external factors will impact crocodiles and their behavior (Hutton 1987; Van Weerd et al. 2006; Somaweera et al. 2019).

Documenting behavior of wild crocodylians can enhance conservation (Garrick and Lang 1977; Thorbjarnarson 1989; Vliet 1989; Thorbjarnarson et al. 2006). Activity budgets provide a link to the bioenergetic budget of species and is a potential tool for assessing mounting environmental and human influences by quantifying changes in energy expenditure (Christiansen et al. 2013). Activity budgets also provide insight into seasonal differences, micro-habitat use, interactions among individuals, and foraging behavior (Hutton 1987, Van Weerd et al. 2006). Time activity budgets have been conducted for a diversity of species (Kemp and Begg 2001; Rahman et al. 2017; Goodman et al. 2019), including Philippine Crocodile (*Crocodylus mindorensis;* Van Weerd et al. 2006) and Nile Crocodile (*Crocodylus niloticus*; Hutton 1987), but to the best of our knowledge, no time activity budgets have been conducted on wild American Crocodiles anywhere in their range. Because time activity budgets have not previously been calculated, and because previous behavioral studies in Belize have focused primarily on reproductive behavior (Platt and Thorbajarnarson 2000b), we sought to establish the first-time activity-budgets for wild American Crocodiles related to season and diurnal period.

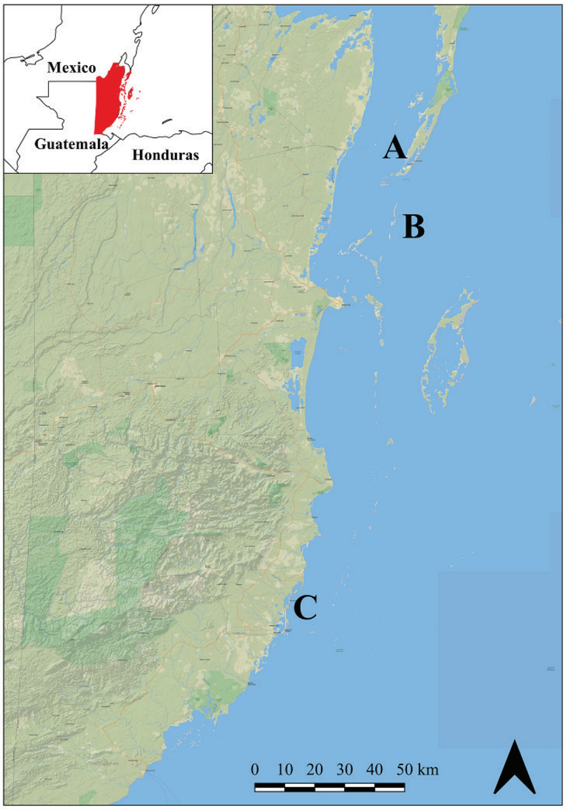

Figure 1. Belize, Central America, located on the eastern Caribbean seaboard. Letters indicate study area location; (A) Ambergris Caye, (B) Caye Caulker, (C) Belize Aquaculture Limited.

Materials and Methods

Study sites.—Belize is a small Central American country (22,965 km^2) situated south of the Mexican Yucatan Peninsula and east of Guatemala (Fig. 1). We collected behavioral observations at three areas in the Belize coastal zone; Ambergris Caye, Caye Caulker, and Belize Aquaculture Limited in the Stann Creek district. Ambergris Caye is an extension of the Mexican Yucatan Peninsula separated by a small channel (Guderjan 1995). We collected data from Coco Beach resort lagoon north of San Pedro town, and the San Pedro sewage ponds and Mahogany Bay Village development sites south of town. There are high relative densities (i.e., encounter rates) of crocodiles at all sites ranging from 8–18 crocodiles/km of lagoon and shoreline (Cherie Chenot-Rose, unpubl. report; pers. obs.). Caye Caulker is an offshore island located 8 km south of Ambergris Caye. American Crocodiles are distributed along the entire island and recent population surveys have established a relative density of 2.4 crocodiles/km of shoreline surveyed (Tellez et al. 2016). We obtained observations opportunistically throughout the study area based on accessibility. Belize Aquaculture Limited (BAL) is a large commercial shrimp farm (3,642 ha) located 8.3 km east of the northern tip of the Placencia peninsula. We observed crocodile behavior at the main effluent polishing lagoon, which has high relative density of 11 crocodiles/km (unpubl. data).

Behavioral observations.—We observed American Crocodile behavior throughout Belize during both the wet (June to November) and dry (December to May) seasons. We observed American Crocodiles on Ambergris Caye from May-August 2015, December 2015 to January 2016, and March 2016. Caye Caulker observations were conducted January, March, and August 2016, and BAL observations were completed June-August 2016. The lead author conducted observations to reduce observer bias and reduce the amount of human interaction with crocodiles during observation periods. We observed crocodiles during crepuscular hours as crocodile wariness and behavior was greatly influenced by human presence and artificial lighting at night. This may be due in part to poaching pressure and response to past and concurrent trapping efforts. Additionally, even with the use of a night vision scope, we found the reliability of observations and ability to observe crocodiles in the water at a distance extremely difficult at night. Thus, our observations focused on hours of peak activity in the early morning and evening (Thorbjarnarson and Hernández 1993; Dinets 2011).

Table 1. List of characterized behavior and description of activities observed for American Crocodiles (*Crocodylus acutus*) in Belize, Central America.

Characterized behavior	General categories of activities	Description of activities
Agonistic	Aggression	Negative behavior (competition for non-food items)
		Chasing with aggressive intent
		Physical altercation; Aggressive threat display (jaw clap, tail wag, head oblique tail arched [HOTA], gaping)
Social	Social signaling	Courtship (pair bonding, circling, dorsal rubbing); Submissive posturing (snout lift)
		Alertness indicator (tail lift, back bob, inflated posture)
Maintenance	Basking	On land, whole body exposed; Partially withdrawn from water, dorsal area exposed
		In water, prolonged exposure of full dorsal surface; Stalking prey
	Foraging	Lifting head to consume prey
		Striking out to capture prey
	Submerging	Entire body concealed below surface of the water
	Surface	Head or body exposed and floating stationary at surface
	Swimming	Locomotion in the water

We conducted observations using focal animal sampling following the protocol of Altmann (1974). Our sampling was conducted during approximated 4-h periods to accommodate time for equipment set up and seasonal discrepancies in sunrise and sunset. Our dawn observation periods were 0530–0930 ± 1 h. We conducted our evening observations 1400–1800 ± 1 h. We recorded observations for all individuals estimated to be sub-adult (total length; TL 90–180 cm) or adult (TL > 180 cm; Platt and Thorbjarnarson 2000a) crocodiles visible at the observation site. The lead author determined the age category (sub-adult, adult) by estimating the approximate total length of an individual, based on known lengths of marked individuals, by comparing the size of the crocodile when adjacent to known-sized objects at the study site, and by estimating and then verifying size during nocturnal capture efforts to record morphometric and acoustic data (Boucher et al. 2020). We added or removed crocodiles from the observation record when they entered or left the field of view of the observer. We recorded all (inter)actions for focal individuals in detail as well as behaviors directed at an individual by others. As time is a crucial factor for the determination of time-activity budgets, we recorded the duration of each observed behavior. We classified recorded behaviors into three categories: Maintenance, Social, and Agonistic with multiple sub-categories (Table 1). At the start and end of each sample period we recorded air temperature and water temperature at the shoreline 15–30 cm below the water surface, when safe to do so, using a standard mercury thermometer.

Statistical analyses.—We compared the proportion of crocodile time spent on activities between wet and dry seasons and between morning and evening observation periods using a Chi-square test of equal proportion with the Yates continuity correction at a 95% confidence interval. The same protocol was used to perform pairwise comparisons of activities between seasons and times. Because our data did not meet the assumptions of normality or homogeneity of variances, we used the non-parametric Kruskal-Wallis test ($\alpha = 0.05$) to compare mean duration among locations for categorized behaviors and individual activities. We used RStudio version 0.99.902 (RStudio Team 2015) for all statistical analyses.

Results

Behavioral observations.—During observations from May 2015 to August 2016, we recorded 13,983 min of American Crocodile behavior, which produced 815 activity records across all three study areas. The number of animals observed per observation period ranged from 1 to 18 and averaged 7.0 ± 1.14 (standard error). Average ambient air and water temperatures (± standard error) during morning observation periods was 27.8° ± 0.287° C and 29.7° ± 0.382° C and afternoon temperatures were 29.0° ± 0.303° C and 34.6° ± 0.198° C for air and water temperatures, respectively. Overall, American Crocodiles in Belize spent the largest proportion of crepuscular time at the surface (40.1%), followed by basking (31.3%),

Table 2. Time-activity budgets (percentage time spent in each activity) of American Crocodile (*Crocodylus acutus*) behaviors between the wet (June to November) and dry (December to May) seasons Belize, 2015–2016. All Chi-square (χ^2) tests were significant at $P < 0.001$.

		Percentage Time		
Category	Activity	Dry	Wet	χ^2
Agonistic		6.27	0.72	338.8
	Aggression	5.70	0.72	295.2
Maintenance		91.1	98.2	366.2
	Basking	27.8	34.2	66.62
	Foraging	6.57	0.73	359.1
	Submerge	12.6	18.9	103.4
	Surface	41.7	38.8	11.75
	Swim	2.99	5.11	38.97
Social		2.65	1.07	338.3
	Social Signals	2.72	1.48	26.16

Table 3. Comparisons in time-activity budgets (percentage time spent in each activity) for American Crocodile (*Crocodylus acutus*) between the morning (AM; 0530–0930 ± 1 h) and afternoon (PM; 1400–1800 ± 1 h) observation periods in Belize, 2015–2016. All Chi-square (χ^2) tests were significant at $P < 0.001$.

		Percentage time		
Category	Activity	AM	PM	χ^2
Agonistic		1.32	6.17	249.7
	Aggression	1.30	5.54	205.7
Maintenance		96.2	93.0	71.31
	Basking	22.1	45.3	835.8
	Foraging	4.60	1.53	95.20
	Submerge	17.7	13.6	41.33
	Surface	46.0	31.2	302.0
	Swim	5.50	2.11	95.58
Social		2.44	0.79	50.78
	Social Signals	2.89	0.76	74.97

submerged (16%), and swimming (4.2%). Foraging (3.4%), aggression (3.0%), and social signaling (2.0%) contributed to the smallest overall proportions of crocodile activity. Crocodiles spent the highest overall proportion of time performing maintenance activities (95.0%) followed by agonistic behaviors (3.2%), and social interactions (1.8%). Proportion of time spent on all activities differed significantly seasonally (Table 2) and temporally (Table 3).

American Crocodiles in Belize spent proportionally greater time on maintenance activities during the wet season than in the dry season (Table 2) and during the morning crepuscular period than during the afternoon (Table 3). Particularly, crocodiles spent significantly more time basking during the wet season (Table 2) and during afternoon periods (Table 3). Conversely, crocodiles engaged in significantly higher proportions of time spent on agonistic and social behaviors during the dry season (Table 2). Significantly more time was devoted to performing agonistic behaviors during the afternoon crepuscular period, while socials signals were significantly higher throughout the morning period (Table 3). Of note, we observed crocodiles in Belize devoting significantly more time to foraging during the dry as opposed to the wet season (Table 2).

Overall mean durations of activities by American Crocodiles differed significantly during the dry season ($H = 84.85$; df = 6; $P < 0.001$), wet season ($H = 126.6$; df = 6; $P < 0.001$), morning ($H = 73.05$; df = 6; $P < 0.001$), and afternoon ($H = 127.68$; df = 6; $P < 0.001$) observations. American Crocodiles spent a greater duration of time in agonistic behavior during the dry than the wet season ($H = 7.036$; df = 1; $P = 0.008$; Table 4) and during the afternoon ($H = 11.380$; df = 1;

Table 4. Mean ($\bar{x}$) duration of time spent (minutes) in various behaviors recorded using time-activity budgets during wet and dry season observations of American Crocodiles (*Crocodylus acutus*) in Belize, 2015–2016. Means followed by asterisk denote significance differences in time spent between dry and wet seasons ($P < 0.05$).

		Dry Season			Wet Season		
Category	Activity	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Agonistic		66	6.03*	0.64	32	1.72	0.14
	Aggression	63	5.75*	0.65	34	1.62	0.14
Maintenance		217	26.7*	2.21	444	17.0	1.08
	Basking	37	47.6	2.48	57	45.8	1.64
	Foraging	25	16.7	0.78	6	9.33	0.77
	Submerge	44	18.1*	1.22	137	10.6	0.65
	Surface	76	34.8*	2.85	191	15.6	0.98
	Swim	37	5.14	0.34	51	7.82	0.39
Social		33	5.09	0.58	23	3.57	0.19
	Social Signals	34	5.09	0.57	23	4.91	0.32

Table 5. Mean ($\bar{x}$) duration of time (minutes) spent in various behaviors recorded using time-activity budgets during morning (AM; 0530–0930 ± 1 h) and afternoon (PM; 1400–1800 ± 1 h) observations of American Crocodiles (*Crocodylus acutus*) in Belize, 2015–2016. Means followed by asterisk denote significance differences in time spent between morning and afternoon observation periods ($P < 0.05$).

		AM			PM		
Category	Activity	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Agonistic		53	2.10*	0.23	45	7.60	0.74
	Aggression	53	2.08*	0.23	44	6.98	0.75
Maintenance		439	18.6	1.16	222	23.2	2.15
	Basking	42	44.4	1.64	52	48.3	2.45
	Foraging	23	16.9	0.62	8	10.6	0.88
	Submerge	121	12.4	0.68	60	12.5	1.14
	Surface	186	21.0	1.32	81	21.4	2.41
	Swim	64	7.37	0.38	24	4.88	0.18
Social		41	5.02	0.42	15	2.93	0.11
	Social Signals	44	5.55	0.44	13	3.23	0.10

$P < 0.001$; Table 5). We found that mean duration of maintenance behavior was significantly greater during the dry than the wet season ($H = 6.827$; df = 1; $P = 0.009$; Table 4) but did not vary by time of day ($H = 0.968$; df = 1; $P = 0.325$; Table 5). Mean duration of social behavior did not significantly differ between seasons ($H = 2.977$; df = 1; $P = 0.085$) and time ($H = 0.968$; df = 1 ; $P = 0.325$). Mean duration of time spent at the surface ($H = 5.419$; df = 1; $P = 0.020$) and time spent submerged was significantly greater during the dry than the wet season ($H = 11.27$; df = 1; $P < 0.001$; Table 5). Seasonal duration means for basking, foraging, and swimming were not significantly different ($H = 0.035$–2.560; all dfs = 1; all $P > 0.050$; Table 4). All other behavior means (basking, foraging, submerging, loafing at the surface, swimming, social signaling) did not differ between morning and afternoon observation periods ($H = 0.007$–1.915; all dfs = 1; all $P > 0.050$; Table 5).

Discussion

Our results are the first to detail variation of activity levels for wild sub-adult and adult American Crocodiles. We found crepuscular crocodile activity were proportionally dominated by maintenance behaviors sustaining daily biological function such as basking, foraging, submerging, and swimming. Of the maintenance behaviors observed, foraging accounted for the smallest proportion of activity. We did not readily observe American Crocodiles foraging during diurnal hours; foraging is generally considered to be a nocturnal activity for crocodylians (Alvarez del Toro 1974; Thorbjarnarson 1989; Nifong et al. 2014). Evidence from our study further infers that both proportion of time, and duration, spent foraging is greater during the dry season and in the morning period. These results align with foraging behavior noted by Nifong et al. (2014) that foraging success for the American Alligator (*Alligator mississippiensis*) is highest in the morning. Furthermore, during the dry season, prey availability may increase as a result of diminished water levels. Crocodylians have been observed capitalizing on these opportunities (Thorbjarnarson 1993; Laverty and Dobson 2013) and increases in time spent foraging during the dry season in Belize may be representative of crocodiles exploiting prey vulnerability.

During observations, fish and crustaceans were found to be the most prevalent prey source for sub-adult and adult American Crocodiles in Belize (Platt et al. 2013; pers. obs.). In spite of abundance at some field sites, we observed only two instances of birds, a Double-crested Cormorant (*Phalacrocorax auritus*) and a Cattle Egret (*Bubulcus ibis*), being consumed by crocodiles. Occasionally, we observed unenthusiastic (i.e., slow unsustained movement towards prey) attempts by adult crocodiles to prey on shorebirds and wading birds, and we often sighted birds within 1 m of crocodiles both in and out of the water. Interactions between wading birds and American Alligators show that some wading birds actively choose sites with alligators as they function as effective nest protectors (Burtner and Frederick 2017). At the observation sites for this study, nesting habitat for wading birds is, in some areas, located adjacent to the shoreline. The diet of American Crocodiles in Belize, however, is comprised predominantly of fish and crustaceans (Platt et al. 2013), indicating that although wading birds are abundant, predation may not be common. It is likely that the predation of birds that does occur is opportunistic or more frequent during nocturnal feeding times when crocodiles are less conspicuous.

Basking was the second most common activity and was the most obvious of the observed behaviors.

Although temperature requirements are not well defined for adult and sub-adult American Crocodiles (Thorbjarnarson 1989), crocodiles bask as the primary means for thermoregulation similar to other ectothermic organisms (Smith 1979). In Belize, crocodiles spent a higher proportion of their activity budgets basking during the wet season. This pattern is likely explained by potentially increased thermal requirements during periods of reduced temperatures and sun exposure from increased precipitation. Further, our observations show that crocodiles exploit thermal advantages by increasing the proportion of time spent basking during afternoon hours, the period with maximal daytime temperatures. Crocodiles will change their behavior to adapt to environmental factors that alter ambient temperatures (Lang 1978). Our observations in Belize infer basking is dynamic and crocodiles tailor activity budgets in relation to temporal and seasonal variation, a factor that may be altered by global trends in climate change.

Time spent resting at the surface, also a proportionally dominant behavior, differed between seasons and time of day. Crocodiles spent a greater proportion of their time resting at the surface during the dry season and morning hours. During the dry season, lack of precipitation and increased diurnal temperatures may impose thermal thresholds on crocodile activity, suggesting crocodiles spend more time resting in the water to ensure thermoregulation. Conversely, during morning hours, and decreased temperatures, crocodiles remain in the water, as we observed lower ambient air and water temperature in the morning.

In relation to temperature, there were marked increases in crocodiles submerging and time spent submerged as daytime temperatures increased. A study of Australian Freshwater Crocodile (*Crocodylus johnstoni*) diving behavior found that waterhole temperature remained consistent while surface temperatures fluctuated, and that diving behavior increased from the morning into the afternoon (Campbell et al. 2010). Similarly, results from this study show that crocodiles spent proportionally more time submerged during the morning than in the afternoon, although duration of time spent submerged were similar between morning and afternoon periods. Records of American Crocodile behavior in Mexico also note that adult crocodiles conceal themselves in deep water during periods of high daytime temperature (Alvarez del Toro 1974).

Agonistic behavior observed for crocodiles in Belize occurred predominantly (both proportionally and in duration) during the dry season. The observed behavior aligns with American Crocodile ecology in Belize as crocodiles breed during the dry season, February to March (Platt and Thorbjarnarson 2000b) with courtship behavior observed in Belize as early as December (pers. obs.). The American Crocodile is polygynous, and male crocodiles defend and compete for breeding territories (Garrick and Lang 1977; Lang 1989; Thorbjarnarson 1989). Male crocodiles observed during captive studies (Garrick and Lang 1977; Lang 1989), in Mexico (Alvarez del Toro 1974), and at our study in Belize, were observed to lounge and chase each other during breeding associated combat. Agonistic behavior observations occurred more during the afternoon observation periods, while social signaling was greatest during the morning period. American Crocodiles increased courtship vocal signaling during morning hours and courtship assemblies disperse during the night (Thorbjarnarson 1989). American Crocodiles in captivity employed more appeasement behavior during courtship in comparison to other species observed (Garrick and Lang 1977; Lang 1989). This appeasement behavior, often post-copulatory, is thought to decrease aggression during the breeding season and protect vulnerable conspecifics, specifically gravid females and juveniles, from agonistic interactions that may cause bodily harm (Garrick and Lang 1977). We did not observe copulation during diurnal hours; however, we observed and recorded associated agonistic behavior and social behaviors. It may be that agonistic behavior increased into the evening as crocodile activity increased and copulation occurred during the night. Thus, during morning hours, social signals increased, as they are post-copulatory appeasement behaviors and courtship behaviors.

Crocodiles observed during our study moved throughout aquatic and wetland habitat at the field sites. Generally, the population at each site remained fairly constant with some individuals moving between the study site and adjacent habitat. The majority of crocodiles present, however, appeared to hold a territory and returned to use the same places during the day to bask, seek shade, and forage. During observations, crocodiles spent a small proportion of time swimming. The greatest proportion of time spent swimming occurred during the morning observation periods and during the wet season. It is likely that crocodiles moved more in the morning as they returned from foraging to return to areas to bask or seek thermal refuge to pass the day.

Conclusions.—This study establishes the first time-activity budgets for American Crocodiles. Proportion of time allotted for recorded activities differed between seasons and daily observation periods. Activity budgets provide a link to understand the bioenergetic investments of wildlife. Our study, as well as studies on other crocodylians in the wild and captivity shows that crocodylians are dynamic and adapt activity budgets to fulfill biological and thermal requirements. Climatic factors, particularly related to ambient temperatures, affect crocodylian activity. In the face of climate change and extensive changes to natural habitats, it is possible that crocodiles will need to adapt their activity budgets to account for environmental changes. This may have an overarching influence on foraging, courtship and breeding, social behavior, and general fitness. Thus, behavior and activity budgets should be integrated into conservation measures and activity budgets considered as a low-cost tool to quantify broad impacts to crocodylian ecology.

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