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Assessment of the American crocodile (*Crocodylus acutus)* population in Ambergris caye, Belize

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Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism and intellectual property.

Ciarán Ó Mórdha

May 21, 2024

Abstract

American crocodiles (*Crocodylus acutus)* have the second largest global distribution of all extant crocodilians, ranging from South Florida through Hispaniola, Cuba, and Jamaica, along the Caribbean coast from southern Mexico to Venezuela, and along the Pacific coast from Mexico to Peru. The species is considered Vulnerable by the IUCN throughout its range, with habitat loss currently a major threat facing the species in parts of its range, including Belize. In Belize, *C. acutus* is found throughout the coastal zone. Ambergris caye, the country's largest and most densely populated caye, is inhabited by *C. acutus*, but its present status there is poorly understood. The aim of this study was to address these data gaps by assessing the status and life history of *C. acutus* on Ambergris caye and comparing this information with that from other areas within the species' range to inform the development of a local American crocodile management plan.

During 19 nocturnal eyeshine surveys covering 171.5 km of shoreline on Ambergris caye carried out between May and September 2023, 199 American crocodiles were observed, an encounter rate of 1.16 crocodiles/km consisting of 22% adults, 10% subadults, 16% juveniles, 22% yearlings/hatchlings and 30% whose size class could not be determined. These results were similar to those of previous surveys carried out in 2010-2011, but with a higher encounter rate in 2023, suggesting a stable, if not slowly increasing, population. Crocodile nests were located by visiting previously identified nest sites, conducting additional surveys by boat and drone, and utilising social media to investigate reports of nesting activity by residents. A total 9 nests were found during the study. More than half (56%) of these were concentrated along the sand banks adjacent to the caye's three sewage treatment ponds. Utilizing the 13 years of crocodile capture data (n=865) collected by ACES Wildlife Rescue in Ambergris caye, this study investigated growth rates, morphometrics, and sexual size dimorphism of the local crocodile population. Analysis revealed the growth rate (total length [TL]) of 115 crocodiles averaged 0.045 ± 0.027 cm/day. The growth rates found in adults differed by sex, with females (n=20) exhibiting a slightly lower average growth rate (0.039 ± 0.028 cm/day) compared to males (n=47) (0.048 ± 0.028 cm/day); however, the difference was not statistically significant. Notably, as total length (TL) increased with age, growth rates slowed more significantly in females than in males, with no significant relationship observed between TL and growth rates in males. Morphometric analysis encompassed 332 juveniles (TL<120cm), 25 female sub-adults (120≤ TL<180 cm), 31 male sub-adults (120≤ TL<180 cm), 40 female adults (TL≥180 cm) and 62 male adults (TL≥180 cm). Allometric relationships between TL and dorscal cranial length (DCL), snout length (SL), snout vent length anterior (SVLa) and snout vent length posterior (SVLp) revealed both positive and negative associations, all of which followed linear regressions. The dorsal cranial length to cranial width ratio (DCL: CW) of 2.7 to 4.2 indicates a broad-snouted skull morphotype akin to that observed in other island populations of *C. acutus* in the Yucatan region. The sexual dimorphism index of 1.07 toward males suggests a relatively minor disparity between the TL of males and females on Ambergris caye,

indicating less pronounced sexual dimorphism compared to other populations of *C. acutus.* The sex ratio 2.39(M):1.0(F) was biased towards males. While Ambergris caye, likely the most human-populated caye in Belize, faces increasing development, pollution, and human-crocodile interactions, it may harbor one of the largest and most stable American crocodile populations in the country. The encounter rate of 1.16 on Ambergris caye is notably higher than that reported for nearby Turneffe atoll (0.34 in 2009) and the Belizean cayes overall (0.43 in 2000), suggesting this population is among the most robust in Belize. However, the study's findings indicate that insufficient nesting habitat could pose a risk to the long-term stability of the population if not addressed through targeted conservation efforts. To mitigate this risk, it is imperative to conduct annual surveys to ascertain long-term population trends. Additionally, implementing protective measures for nests and intensifying surveys within the Bacalar Chico National Park and Marine Reserve to investigate nesting activity are vital steps in formulating a robust species management plan. Addressing these research gaps will not only enhance our understanding of the ecology of *C. acutus* in Belize but also inform targeted conservation efforts essential for safeguarding this population's viability and ecological role in the region.

Overview of thesis

This thesis consists of five chapters. Chapter 1 is a review of the literature concerning the American crocodile (*Crocodylus acutus),* encompassing global research on the species, gaps in our knowledge and insights from previous studies conducted in Belize. It covers various topics such as general biology, ecology, reproduction, hybridisation, conservation status, threats, and geographic distribution.

Chapter 2 explores the physical and biological characteristics of the Ambergris caye study site, in Belize, which serves as a habitat for the American crocodile.

Chapter 3 presents a comprehensive demographic assessment of the crocodile population, including current encounter rates and extensive surveys of population structure, such as size class distribution, habitat preferences, and nesting site locations. The primary objectives of this chapter was to establish baseline data for future monitoring efforts and to assess whether the population is experiencing decline, stability, or growth.

Finally, Chapter 4 conducted an analysis of 13 years (2011-2023) of data collected by the locally based ACES Wildlife Rescue organization to elucidate various aspects of population growth and characteristics, including sex ratios, sexual size dimorphism, growth rates, and biometric and morphometric measurements. The overarching goal of this chapter is to leverage current and historical data to provide quantitative insights tailored to the ecological context of the Ambergris caye American crocodile population.

Chapter 5 considers the main findings of this research, identifies their implications for the continued survival of American crocodiles on Ambergris caye, and suggests ways in which research can be expanded in the future.

Chapter 1

General introduction to the American crocodile

(*Crocodylus acutus)*

Taxonomic classification

American crocodiles belong to the order Crocodylia in the clade Archosauria. Crocodilians are large, powerful, semiaquatic reptiles with short legs, webbed feet, powerful tails, and tough, armoured scales covering the dorsal surface. Crocodilians are almost exclusively carnivorous (Gignac et al., 2019, but see Platt et al., 2013), and their diet consists of fish, mammals, birds, other reptiles, amphibians, crustaceans, insects, and other invertebrates (Grigg and Kirshner 2015).

The order Crocodylia has fossil record evidence dating back to 95 million years (Brochu, 2000). The closest living relatives to crocodilians are birds, in the class Aves. Crocodilians have had a long and diverse evolutionary history, with many extinct species adapting to a variety of habitats and niches such as the terrestrial *Quinkana fortirostrum and Mekosuchus species*, and the entirely marine Metriorhynchidae crocodylomorphs (Hutchinson et al., 2019; Wilberg et al., 2019). The oldest fossil evidence for Crocodylia date back to ~100 million years (Oaks, 2011). There are currently 26 extant recognised species of crocodilians (Hekkala et al., 2011; Shirley et al., 2014), though this is likely to increase, as a result of genetic evidence which supports the recognition for two additional species, *Osteolaemus aftezelli* and *Crocodylus halli*, which have yet to be formally recognised (Shirley et al., 2018). The 26 extant species belong to three separate families known as the Alligatoridae, Gavialidae and Crocodylidae (Norell, 1989; Grigg and Kirshner 2015).

The family Alligatoridae contains all extant alligator and caiman species. There are two species of alligator, the American (*Alligator mississippiensis*) and Chinese (*A. sinensis*) alligator. Alligators have adapted to tolerate cooler temperatures which have allowed them to thrive in habitats much further north of the equator where their ability to enter hibernation during the coldest parts of the year would be intolerable for other crocodilians (Wang et al., 2014; Zhang et al., 2021). The caimans are comprised of three genera and six extant species, all of which are found in South America and Central America having adapted in jungle freshwater habitats and niches (Zhang et al., 2021); The Chinese alligator is the only species in the family found outside the Americas. Alligators can be distinguished morphometrically from caimans by the presence of a bony septum dividing the nostrils and the lack of ventral armour possessed by caimans (Bona and Desojo, 2011). Both alligators and caimans have notches in the maxilla that fit the mandibular teeth (Bona and Desojo, 2011); and salt glands are absent from the tongues of Alligatoridae (Taplin et al., 1982).

The Gavialidae and Crocodylidae belong to the Longirostres clade (Perrichon et al., 2023). The Gavialidae contain two extant species, The Gharial which is found in Nepal and India where its population is highly segmented (Thapaliya et al, 2009; Panda et al., 2023). The False Gharial (*Tomistoma schlegeliiI),* also commonly referred to as Tomistoma, is native to Indonesia, Malaysia, Brunei and Thailand (Stuebing et al., 2006) and has historically been placed in the Crocodylidae family based on morphological evidence. However, due to genetic (Harshman et al., 2003) as well as

morphological evidence during early development Piras et al (2010) in 2018 the False Gharial was recognised as belonging in the family Gavialidae by the Crocodile Specialist Group (CSG), though research is still being conducted to support both placements. Gavialidae, especially the gharial, show the most extreme jaw structure, being extremely long and slender with little to no tapering. Both species have salt glands present on the tongue (Perrichon et al., 2023).

The Crocodylidae, the most diverse family of extant crocodilians, are commonly known as the true crocodiles; having 16 currently recognised extant species (Shirley et al., 2014). Crocodylidae has the widest distribution of all crocodilian families, present in Australia, Southeast Asia, the Middle East, Africa and the Americas. The Crocodylidae contains two sub-families, the Osteolaeminae and the Crocodylinae (Meganathan et al., 2010). The Osteolaeminae contains two clades, though this may change as more evidence is gathered, and currently includes 4 extant species, the slender snouted and dwarf crocodiles (Shirley et al., 2014; 2018).

The sub-family Crocodylinae, to which the American crocodile belongs, is the most diverse of all extant crocodilian lineages (Man et al., 2011), and is comprised of 12 extant species. Like all Crocodylidae, species within the Crocodylinae can be distinguished generally by their exceptionally large fourth mandibular teeth, which are exposed when the mouth is closed, passing through a furrow in the top jawbone (see Figure. 1.1). All Crocodylidae have salt glands present on the tongue and integumentary sensory organs (ISOs) around the head, but unlike the Alligatoridae ISOs are also present along the body of the Crocodylidae (Leitch and Catania, 2012).

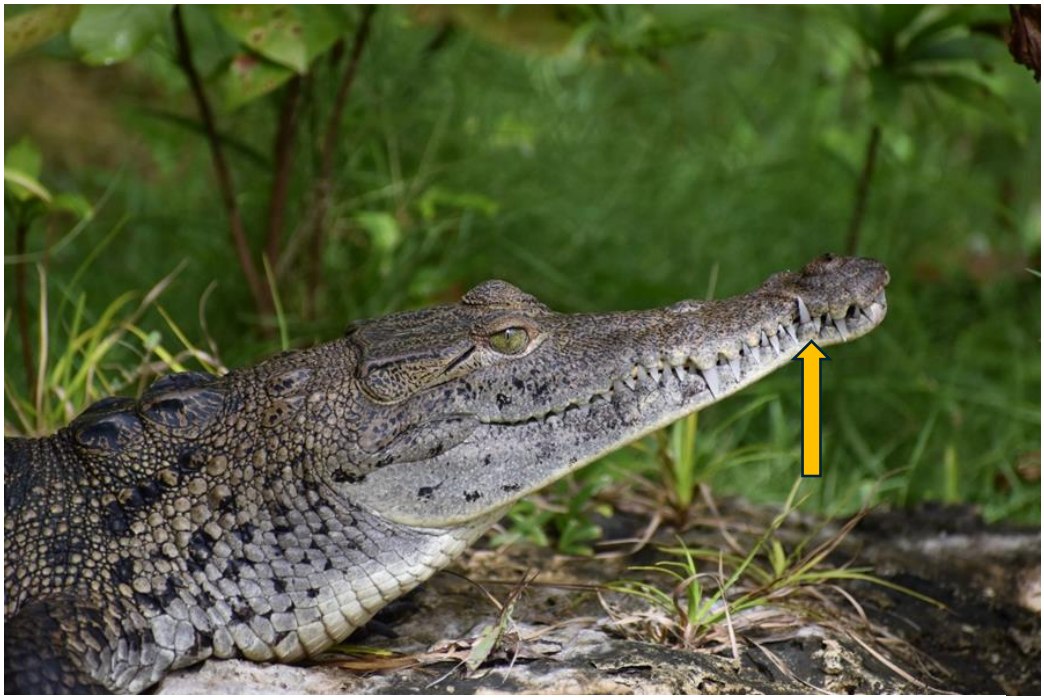

Figure 1.1. A *Crocodylus acutus* on Ambergris caye, Belize illustrating the prominent and visible 4th mandibular tooth. Source: Ciarán Ó Mórdha

Species description of the American crocodile

The American crocodile is a large crocodilian with a relatively narrow, tapered jaw. Colouration and patterning are highly variable, but generally of earthy tones ranging from olive green to much darker greens (see Figure 1.2). Hatchlings and juveniles tend to have much more contrasting colours of lighter green with black striping especially on the tail (Thorbjarnarson, 1989). The ventral side is much paler, generally creamy white or yellow.

The skull morphology of *C. acutus* appears to be highly variable as a result of ecological factors. For example, with regard to diet, short and broad snouts are favoured for more hard-bodied prey, while long and narrow snouts are favourable for faster, more agile prey (Labarre et al., 2017). The body mass of individuals appears to be highly variable, influenced by environmental and geographic factors as well as intra- and inter-specific interactions leading to observed morphological differentiation (Rainwater et al. 2010). Individuals longer than four metres are rare. This may be due to inaccurate measuring and data recording methods leading to overestimates of size, as well as historic exploitation of the species for the skin trade and meat (Kushlan and Mazzotti, 1989; Thorbjarnarson, 1989).

American crocodiles display sexual dimorphism, with adult males generally reaching larger sizes than adult females (Platt and Thorbjarnarson, 2000a; 2000b; Charruau et al., 2010). Size at sexual maturity for males differs by location and is difficult to determine but is most likely ≥ 2m total length (TL). More recent studies place minimum reproductive size for females and males, which was chosen for this study (see Chapters 3 and 4), at 180 cm TL (Balaguera-Reina et al., 2015; Labarre et al., 2017). While there is much overlap in the size of males and females, individuals larger than 3.5 metres are rarely female, and the largest individuals in populations tend to be male (Throbjarnarnson, 1989).

American crocodiles, like all Crocodylidae, have integumentary sensory organs (ISOs) present on scales on the head as well as along the ventral and anterior middle portion of the body scales (Leitch and Catania, 2012). They have the most reduced and irregular arrangement of dorsal osteoderms, which are hard bony scales embedded within the skin. These osteoderms typically feature no more than 4 scutes in any of the 14-17 continuous precaudal scute rows (see Figure. 1.3) (Platt et al., 2012; Platt and Rainwater, 2005). The American crocodile is also unique in the degree of development of a preorbital ridge (PR) on the snouts of adults and sub-adults (see Figure. 1.4**)** (Thorbjarnarson, 1989). Although it is variable geographically and size appears to be sexually dimorphic, males having relatively larger PRs. It is distinctive from other crocodilian species with only the Morelet's crocodile displaying a similar feature, but to a lesser degree (Platt and Rainwater, 2005).

Recent genetic studies have confirmed that significant hybridisation is occurring between *C. acutus* and *C. moreletii* in the coastal zone of Belize (Hekkala et al., 2015; Wilkie et al., 2024) and Mexico (Cedeño-Vázquez et al., 2008; Machkour-M'Rabet et al., 2009) as well as with *C. rhombifer* in Cuba

(Milián-García et al., 2015; 2018). The ecological and evolutionary consequences of this hybridisation are poorly understood but are a priority for future work.

Hybridisation with non-native *C. moreletii* that became established after escaping from commercial crocodile farms potentially threatens the genetic integrity of *C. acutus* in some areas along the Pacific coast of Mexico (Serrano-Gómez et al., 2016; Pacheco-Sierra et al., 2018). Although along the Yucatan mainland of Mexico there is extensive hybridisation between *C. moreletii* and *C. acutus* (Cedeño-Vázquez et al., 2008; Hekkala et al., 2015; Wilkie et al., 2024), the island populations on Cozumel and Banco Chinchorro remain genetically pure (Machkour-M'Rabet et al., 2009; Pacheco-Sierra et al., 2018). An isolated population of *C. acutus* occurs in the Rio Grijalva, the only known Gulf of Mexico drainage where the species is present. In the Grijalva drainage, crocodiles inhabit a series of freshwater reservoirs, as well as riverine habitats between reservoirs (Sigler, 2002).

Across the Antilles range of *C. acutus* hybridisation appears to have been ongoing historically between *C. acutus* and *C. rhombifer* (Milián-García et al., 2015). Research into the genetics comparing the population of *C. acutus* in the Antilles against continental population suggest the current taxon *C. acutus* is more likely a complex of cryptic species that may need reassessment (Milián-García et al., 2018). The latter study also suggests that *C. acutus* western population in Cuba may be a transitory zone between two distinct lineages.

Figure 1.2. A *Crocodylus acutus* on Ambergris caye, Belize showing the pattern and colour change on the ventral and dorsal sides of the body. Source: Ciarán Ó Mórdha.

Figure 1.3. A *Crocodylus acutus* on Ambergris caye, Belize illustrating the arrangement of dorsa. Source: Ciarán Ó Mórdha.

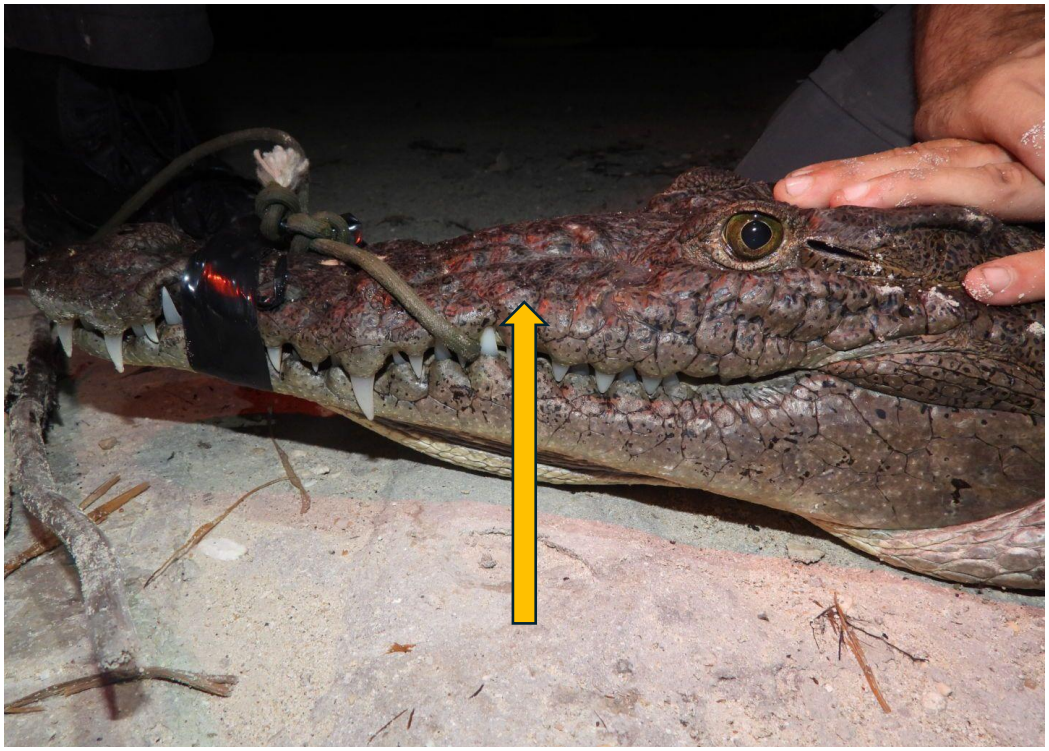

Figure 1.4. A *Crocodylus acutus* on Ambergris caye, Belize illustrating the well-developed preorbital ridge, unique to the species. Source: Ciarán Ó Mórdha.

Global geographic distribution and range-wide status

Figure 1.5. Map of geographic distribution range of *Crocodylus acutus*. (Adapted from the IUCN website).

The American crocodile has the widest distribution of any crocodilian in the New World and second-widest distribution world-wide, with only the Indo-Pacific crocodile (*Crocodylus porosus)* having a larger distribution. Both species have very well-developed salt excretion glands (Taplin et al., 1982) allowing them to tolerate saline environments and swim greater distances in marine systems than other crocodilians. This tolerance for salinity removes the open ocean as a barrier to dispersal for both species, as evidenced by their presence along the coasts and islands of their range (see Figure 1.5) (Cherkiss et al., 2014; Mazzotti et al., 2019; Rainwater et al., 2019).

The Crocodile Specialist Group (CSG) conducted an assessment for the IUCN Red List of threatened species in 2020. American crocodiles are listed as Vulnerable under criteria A2cd; A2 indicates that the taxon has declined by more than 50% in the last 10 years or three generations (whichever is longer); the subcriteria cd indicates that the decline in mature individuals has been caused by a decline in the quality of habitat as well as actual levels of exploitation. From the review of all reported data as well as expert opinions across the species range, the current number of the mature individuals is estimated to be approximately 5000 (Rainwater et al., 2021). The overall population trend is increasing. Thorbjarnarson et al. (2006) concluded populations were recovering in most parts of its historic range. Colombia and Ecuador were found to be exceptions, the first where recovery was limited, the second non-existent. The populations in the USA, Mexico and Costa Rica appear healthy and robust. Thorbjarnarson et al. (2006) identified 69 areas in eight distinct bioregions as Crocodile Conservation Units (CCUs) defined as critical areas for conservation focus of the populations.

Northern Peru, Southern Ecuador, Northwest, and central Pacific Mexico were recommended as a high priority.

North America and the Antilles

In the United States, the geographic range of *C. acutus* is confined to the southernmost, subtropical region of Florida. Initially listed as Endangered under the US Endangered Species Act in the 1970s, concerted efforts by organizations such as the National Parks Service, Florida Game and Freshwater Fish Commission, and Florida Power and Light Company have shown positive impacts on the species' population. Mazzotti et al. (2007) observed an increasing trend in crocodile numbers and expansion into new habitats, prompting a re-evaluation of its status. Consequently, in 2007, the species was reclassified as threatened (Stansell, 2007). Green et al. (2014) predicted that the implementation of the Comprehensive Everglades Restoration Plan (CERP), despite having some negative impacts to the population, would have a much more favourable outcome for crocodiles than if not implemented across south Florida, with some areas such as Joe Bay having a 30% increase and other areas such as the Buttonwood channel area having a 30% decrease in crocodile population size. Mazzotti et al. (2022) found a *C. acutus* nesting success rate of near 90% across south Florida in 2010 compared to 61% in the 1970s showing a continued improvement in nesting success rates over the past 50 years. Surveys conducted by Cherkiss et al, (2011) along Biscayne Bay and mainland shorelines of Barnes and Card Sounds, Florida, revealed a steady annual rise in crocodile numbers from 1996 to 2005.

American crocodiles inhabit various islands in the Antilles, including Cuba, Hispaniola, and Jamaica (Milián-García et al., 2018). Cuba, in particular, hosts a widespread and abundant population of *C. acutus*, with management efforts such as ranching and closed-cycle captive breeding initiated after its inclusion in CITES Appendix II (Soberón et al., 2002). However, genetic studies suggest the need for reassessment, hinting at the possibility of a cryptic species within the Cuban and Antilles populations (Milián-García et al., 2018).

Historically, *C. acutus* inhabited the Cayman Islands but was considered extirpated. While sightings were rare after 1959, recent reports in 2008-2009 noted the presence of three crocodiles, including a Cuban-American hybrid, likely originating from Cuba (Echternacht, Burton and Blumenthal, 2015). No evidence of nesting or a permanent viable population has been observed to date.

In Hispaniola, encompassing the Dominican Republic and Haiti, *C. acutus* populations exhibit varying trends. In the Dominican Republic, a decline has been observed since the 1980s, with the majority of the population concentrated in the southwestern Lago Enriquillo. Surveys conducted by Greco Jr. et al., (2023) during 2021 suggest that the population is continuing to decline due to hunting, fishing, and habitat destruction but is still present and breeding in Lago Enriquillo. In Haiti, the

species is primarily found in the brackish lake Etang Saumâtre, with limited recent data available and the current status of the population unknown (Thorbjarnarson, 1989).

Jamaica's *C. acutus* population, while historically stable, faces challenges in recent years. Habitat destruction and increased demand for crocodile meat have led to scattered populations and illegal harvesting, posing a threat to the species' survival without effective conservation measures (Hailey, Wilson and Horrocks, 2011).

South America

In Colombia, the population of American crocodiles is on the rise, with new populations discovered across the country. This positive trend led to the species being down-listed from "Critically Endangered" to "Endangered" in the latest local assessment (Morales-Betancourt et al., 2015). Notable populations thrive in various regions, including Portete and Cispatá Bay, Puerto Badel (Arjona municipality), Dibulla, Tayrona Natural National Park, and along rivers such as Sardinata, San Miguel, Nuevo Presidente, and Tibu in the Caribbean region. However, ecological studies have predominantly concentrated on just 37% of the national territories over the past decade, resulting in significant knowledge gaps, particularly concerning the Pacific and Andean regions (Balaguera-Reina, Venegas-Anaya and Densmore, 2014).

In Venezuela, crocodiles inhabit various coastal areas and river systems along the Caribbean coast. Restocking efforts with ranched stock have been successful in Falcon Province and Aragua Province, where active conservation programs, including surveys and monitoring, are in place (Villarroel et al., 2005). Despite interruptions due to military exercises in Turiamo Bay (Hilevski and Velasco, 2020), populations in several locations have remained stable or have shown signs of growth, attributed to protection and restocking initiatives (Velasco, de Sola and Lander, 2000). The Venezuelan government has implemented a National Recovery Plan for *C. acutus,* with proposed Critical Conservation Units (CCUs) primarily located along the Caribbean coast of Venezuela and Colombia (Thorbjarnarson et al., 2006).

Two of the three proposed CCUs encompass mangrove systems located in seasonally dry areas. One such unit is situated in Colombia, specifically in Alta Guajira, comprising Bahía Portete and Bahía Hondita (Thorbjarnarson et al., 2006). The second mangrove CCU is located in Venezuela, cantered around Laguna Tacarigua. Additionally, the Bahía Cispatá CCU constitutes an extensive mangrove swamp linked to the ancient delta of the Rio Sinú. Furthermore, the second tier of priority CCUs includes diverse habitat types. For instance, an inland freshwater riverine site within a dry forest habitat, known as Rio Bache in Colombia, spans over 1200 km from the coast. Additionally, a coastal complex formed by the Yaracuy and Aroa rivers, along with a reservoir, Embalse Pueblo Viejo, are recognized as crucial areas for conservation efforts (Thorbjarnarson et al., 2006).

The Pacific coast of South America presents a different scenario, with populations of *C. acutus* facing significant threats. In Ecuador, crocodiles, once abundant in the Rio Guayas system, are now at risk of extirpation due to habitat destruction caused by shrimp aquaculture facilities (Carvajal and Alava, 2005). Similarly, mangrove destruction for aquaculture poses a threat to crocodile habitat in the coastal region of the Gulf of Guayaquil. In northern Peru, a small population persists in the Rio Tumbes region, marking the southernmost limit of the species' range (Trelancia, 2001). Efforts to conserve these populations include identifying Critical Conservation Units (CCUs), such as the Amotape CCU and Estero Corrales, both associated with the Rio Tumbes drainage (Thorbjarnarson et al., 2006). Despite their designation, these areas remain threatened by activities such as shrimp aquaculture and rice farming.

Central America

Along the Pacific coast of Mexico, American crocodiles inhabit suitable habitats extending from the Guatemalan border to the State of Sinaloa (Huerta, Ponce Campos and Ross, 2002; Machkour-M'Rabet et al., 2009). Notable reports have originated from various states, including Jalisco, Sinaloa and Oaxaca (Navarro Serment, 2003; Garcia-Grajales, Buenrostro-Silva and Charruau et al., 2012). Within this bioregion, the three primary CCUs often comprise coastal landscapes characterized by small mangrove areas near river mouths, as seen in the Jalisco-Colima coast, or coastal lagoon/mangrove complexes with intermittent freshwater inputs, exemplified by Bahía de Petacalco and the Oaxaca coast (Thorbjarnarson et al., 2006).

Crocodiles are found across these fragmented habitats, with sightings reported in 38 out of 52 water bodies along the Jalisco coast alone (Huerta, Ponce Campos and Ross, 2002). Additionally, crocodile populations thrive in inland reservoirs like Presa Adolfo López Mateos, identified as a CCU, and in freshwater sections of major rivers such as the Rio Santiago CCU (Thorbjarnarson et al., 2006). Concerns arise regarding hybridisation with *C. moreletti*, escaped from crocodile farms along the Pacific coast.

In the 1980s and 1990s, *C. acutus* populations in Guatemala were significantly diminished, as reported by Thorbjarnarson (2010), yet current data from the region remains scarce. Similarly, crocodile sightings are infrequent in El Salvador. Escobedo-Galván's (2004) spotlight surveys conducted in 2002, in prime coastal habitats, revealed only 28 crocodiles, primarily juveniles, along a total surveyed distance of 157.5 km, resulting in an encounter rate of 0.17 crocodiles/km. In Honduras, while small populations persist along most major rivers in the Atlantic drainage, many are showing signs of decline (King, Espinal and Cerrato, 1990). Cerrato's (2002) surveys in northern coastal Honduras, focusing on wetlands linked to Laguna Guaimoreto, Rio Chapagua, Laguna El Lirio, and the lower 15 km of Rio Aguan, recorded an average encounter rate of two crocodiles/km. This indicates an increase compared to surveys from 1989 in the same area. Notably, the El Cajon

Reservoir hosts perhaps the largest crocodile population in Honduras, with 1,082 individuals counted, including a substantial number of hatchlings (536), affirming successful breeding (Espinal and Escobedo-Galván, 2011). Furthermore, crocodiles have been observed breeding on certain Bay Islands off Honduras's northern coast (Kaiser, Sihotang and Crane, 2001).

In Nicaragua, surveys conducted by King, Ross and Gutierrez (1994) reported *C. acutus* as rare but still persisting in the Atlantic drainage, while several viable populations were identified on the Pacific coast, including areas such as Estero Real, Las Salinas, and near Managua. Similar findings were found by Buitrago (2000). The incidental illegal take of crocodiles, often associated with legal caiman harvesting, remains a concerning issue.

Costa Rica exhibits a low density of crocodiles in wetlands along the Atlantic coast, whereas higher density populations are observed in mangrove swamps and rivers along the Pacific coast (Mauger et al., 2012). Notable populations include over 300 individuals reported from the Rio Grande de Tarcoles and about 35 individuals in Estero Roto (Sasa and Chaves, 1992; Chaves Cordero, 1993). Moderate encounter rates were recorded in various locations, including the Rio Chirripó at La Rambla de Sarapiquí, Golfo de Nicoya, and mangrove wetlands associated with the Terraba and Sierpe rivers (Bolaños, Sánchez R and Piedra C, 1996). Growing populations of crocodiles alongside human settlements in Costa Rica have resulted in instances of human-crocodile conflict, including fatal attacks (Sandoval-Hernández, Duran-Apuy and Quirós-Valerio, 2017; Murillo and Cambronero, 2020).

Exposure to environmental contaminants poses significant risks to the health and ecology of *C. acutus*. Synthetic sex steroids, including novel environmental androgens, have been detected in this species, suggesting endocrine disruption potentially linked to aquaculture and industrial pollutants (Murray et al., 2017). Additionally, elevated levels of metals and organochlorine pesticides have been documented in caudal scutes of individuals from Belize and Costa Rica, implicating agricultural and industrial runoff as major sources of contamination (Rainwater et al., 2007). Chronic exposure to these pollutants has been associated with adverse health effects, such as ocular pathologies, including cataracts, highlighting the broader ecological consequences of pollutant bioaccumulation in crocodilian populations (Rainwater et al., 2011).

In Panama, a long-term study on Coiba Island has provided valuable insights into the population genetics, reproductive, spatial, trophic, and population ecology of American crocodiles inhabiting insular areas (Bashyal et al., 2014; Balaguera-Reina et al., 2015; Balaguera-Reina et al., 2016; Balaguera-Reina et al., 2018). An estimated population size of around 200 non-hatchlings on the southern tip of the island has highlighted the importance of Coiba Island as a hotspot for American crocodiles.

In the regional analysis conducted by (Thorbjarnarson et al., 2006), the highest priority CCUs in the Caribbean drainage of Central America encompass very different habitats, including extensive regions of eastern Nicaragua (Costa Miskito and Rio Coco), a section of Lake Nicaragua, and a region of central Caribbean Panama (Bahía de Panama-Este). Along the Pacific coast, high-priority CCUs are characterized by patches of coastal mangrove and short sections of estuarine rivers, such as Puerto Sandino and Estero Real in Nicaragua. Isla Coiba in Panama, a national park comprising 40 islands, is also highlighted as an important area for robust populations of *C. acutus* associated with rivers and coastal mangroves. Similarly, robust populations are found along the Pacific coast of Costa Rica, particularly in the Rio Terraba and Rio Tempisque areas, which were rated at the second CCU priority level (Thorbjarnarson et al., 2006).

Belize

The largest populations of *Crocodylus acutus* in Belize are located on islands along the mainland, including Turneffe atoll, Ambergris caye, and Caye Caulker. However, these populations face significant threats from rapid wetland habitat loss caused by human development (Rainwater and Platt, 2009; Chenot-Rose, 2013; Tellez, Boucher, and Kohlman, 2016). In addition to habitat loss, Wu et al. (2000) investigated the presence of DDE, a persistent metabolite of the pesticide DDT, in the eggs of two crocodile species in Belize. Their findings revealed measurable concentrations of DDE residues, indicating environmental exposure to organochlorine pesticides. This exposure poses potential risks to reproductive health and embryonic development in crocodilians due to the bioaccumulation of these persistent pollutants in their habitats.

These island habitats, particularly on Ambergris caye and Caye Caulker, are not suitable for *C. moreletii* due to higher salinity levels. Along the mainland coastal region, both species' ranges overlap to varying extents, leading to regular hybridisation in coastal zones but not on island populations (Hekkala et al., 2015; Wilkie et al., 2024). However, it remains uncertain whether the current degree of hybridisation mirrors historical levels or is influenced by habitat changes. *C. acutus* is absent from riparian inland habitats in the interior.

Four CCUs have been identified in Belize: Bahia de Chetumal, Turneffe atoll, Gales Point, and Lighthouse atoll (Thorbjarnarson et al., 2006). Concerning trends have been observed in Turneffe atoll and Lighthouse atoll since the identification of these CCUs, with a possible decline noted in a population survey conducted in 2008 (Rainwater and Platt, 2009). Although Ambergris caye is not officially recognized as a CCU, it harbours a significant crocodile population (Chenot-Rose, 2013). See Chapter 3 for an assessment of the current population on Ambergris caye, as well as potential risks to the population.

Morphology is a useful method in determining ecological factors such as prey selection, habitat use and intra-specific competition (Platt et al., 2009; Webb and Messel, 1978) especially when focused on crocodilian skull morphology due to its plasticity (Pearcy and Wijtten, 2011; Labarre et al.; 2017). Growth in crocodilians is a useful measure of determining the ecological health of the population (Balaguera-Reina et al., 2015), slow growth rates are commonly shown to be related to poor habitat quality and prey availability as well as potential pollutant exposure (Garcia-Grajales, Buenrostro-Silva and Charruau et al, 2012). See Chapter 4 for an assessment of the morphological and growth characteristics based on 13 years of captures of *C. acutus* on Ambergris caye, Belize.

Life history

Different aspects of the annual activity cycle of adult American crocodiles generally coincide with either the wet season or dry season, which vary throughout the animal's extensive range. Courtship takes place in January and February, though this may vary across the range. Nesting occurs March-May in Mexico, April-May in Florida, and January-February along the Pacific coast of Costa Rica and Colombia (Platt and Thorbjarnarson, 2000a; Charruau et al., 2010; Balaguera-Reina et al., 2015; Charruau et al., 2022). These differences in timing likely reflect behavioural adaptations to differing seasonal climates, thus displaying the American crocodile's reproductive plasticity (Thorbjarnarson, 1989).

Yearlings and juveniles appear to use habitats and areas away from adult populations, displaying an ontogenetic variation in habitat preference (Balaguera-Reina et al., 2018). Growth occurs rapidly for the first two weeks after hatching, with the absorbed yolk providing nutrition for the hatchling until it begins foraging, mainly small fish and aquatic invertebrates. Growth rates slows with age, and the danger of predation dramatically drops in sub-adults and adults (Somaweera, Brien and Shine, 2013).

Breeding success appears to relate to size (Mazzotti, 1989). Though reproductive size varies across American crocodiles range (Mazzotti et al., 2022), both male and females generally achieve reproductive size around 8-10 years (Thorbjarnarnson, 1989)). Recent studies place minimum reproductive size for females and males, which was chosen for this study, at 180cm (Balaguera-Reina et al., 2015; Labarre et al., 2017). Evidence for minimum reproductive size for females appears to reflect a strong impact of environmental and/or genetic differences in growth rates and/or age at sexual maturity. In Cuba the minimum reproductive size is reported as 2.7-3.0 m TL. In areas such as eastern Honduras, Etang Saumâtre the minimum reproductive size for females is much smaller 2.2 – 2.4 m TL with females never reportedly achieving TL >3 m. In Florida Mazzotti (1989) determined a minimum nesting size to be 2.25 m TL.IMinimum reproductive size for males is not well documented (Charruau et al., 2010). The difficulty in determining this is due to the difficulty with collecting sperm samples from live adult males (Murphy and Wilkinson 1982) and relying on size estimates of males during copulation (and determining if those males successfully contributed to fertilised eggs). The

minimum size for reproduction of males is most likely variable geographically through the species range, similar to females (Platt and Thorbjarnarson, 2000a; 2000b)

Reproductive behaviour

Mating systems for American crocodiles are polygynous (Garrick and Lang, 1977; Thorbjarnarson, 1989). Adult males display territorial aggression excluding other males but allowing females to enter for courtship. Male on male aggression stereotypically starts with posturing, lifting the head and tail above the water. Posturing often leads to actual physical confrontation and mock fighting, males will lunge, bite and chase competitors. The dominant male assumes a raised "inflated posture" after combat (Garrick and Lang, 1977; Budd, Spotila and Mauger, 2015).

Mating for American crocodiles is exclusively aquatic. Courtship is generally initiated by the female; a sequence of stereotypical behaviours occurs. Females display snout lifting, swimming around the male in slow circles and placing their head on the body or the head of the male. The response of males is generally characterised by the emission of very low frequency sound known as sub-audible vibration (SAV) (Benko and Perc, 2009). Males generally assume the "head-emerged tail arched" posture. SAVs can lead to the agitation of water upwards above the back termed as the "water dance". The role of vocalisations in American crocodiles is not well understood but bellowing has been reported sparsely in the wild and captivity (Boucher, Tellez and Anderson, 2020).

After this stage the next sequence of behaviours generally observed include, snout lifting and rubbing, bubbling and temporary submergences. Copulation takes place in shallow water lasting usually several minutes. The female submerges below the male orientating the body so that ventral side of the body faces upwards toward the male's ventral side (Charruau et al., 2022).

Aggression between females is also observed. Competition for nesting sites has commonly been reported in parts of their range, though nesting colonially in some regions results in very little territorial aggression (Platt and Thorbjarnarson, 2000b; Budd, Spotila and Mauger, 2015).

Nest site selection

Typically, nests are holes dug into loose substrate (sand, soil) near the water's edge (Platt and Thorbjarnarson, 2000a). American crocodiles have demonstrated a high degree of plasticity in terms of nesting requirements. Mound nests have been documented in Florida using soil, mangrove peat and scraped up vegetative litter (Mazzotti, 1989; Mazzotti et al., 2022). In these cases the female digs a shallow hole with her hind legs, deposits the clutch, and covers the hole with substrate, forming a mound. Overall, mound nests are a rare occurrence for American crocodiles and not significant for the overall nesting ecology of the species. Due to the animals' large range and habitat diversity, the species shows a large variability in nest site selection (González-Desales et al., 2016). Sandy elevated

beaches are the most commonly observed nesting sites and seem to be preferable despite the animal's adaptability (Mazzotti et al., 2022).

Oviposition in wild and captive populations occurs generally 1-2 months following courtship (Platt and Thorbjarnarson, 2000a; Mazzotti et al., 2022). Females approach potential nesting sites 4-6 weeks prior to laying. Visits and exploratory digging take place and their frequency increases closer to oviposition. Digging takes place nocturnally several days pre-oviposition. Females regularly reuse successful nesting sites yearly, though changes to the nesting site conditions, such as rising water levels, often females to relocate to a new site (Mazzotti et al., 2022).

Nesting behaviour

Females will remain in the vicinity of the nest during incubation. Nest site defence appears to be individually and regionally variable (Mazzotti, 1989; Platt and Thorbjarnarson, 2000a). Females in Mexico have been observed actively defending nests from predators (González-Desales et al., 2016). In Florida, females provided little or no nest protection (Mazzotti, 1989; Mazzotti et al., 2022). There is no evidence of males taking part in nest defence.

Females begin nocturnal visits to their nests as the incubation period nears its end. Females will lay their head on the top of the nest, likely listening for release calls from hatchlings. Release calls trigger the female to begin excavating the nest. Females will help with the hatching process by gently squeezing the eggs between the tongue and palate. The female will carry the hatchlings in the depressed gular pouch of the mouth, bringing them to the water's edge, making multiple trips (Charruau et al., 2022).

Maternal care varies considerably through the American crocodile range. The formation of creches of hatchlings and maternal care appears to be minimal (Thorbjarnarson, 1989). This may be due to a number of behavioural environmental and anthropogenic factors. Hatchlings disperse almost immediately in areas where hyper salinity and wave action are a factor. At nesting sites with more favourable conditions for hatchlings, creche formation and maternal care has been observed for several weeks after hatching, but in other instances with similarly favourable conditions creche formation does not occur (Charruau et al., 2022).

American crocodiles are generally quieter than other crocodilians, producing fewer vocalizations (Benko and Perc, 2009). The minimal maternal care currently observed could be a characteristic behaviour for the species, but it's also possible that historic human disturbance has caused a shift in their behaviour (González-Desales et al., 2012; Mazzotti et al., 2022). Hunting pressure might have preferentially targeted larger, more defensive adults, leading to a population skewed towards individuals less likely to guard their nests and young. Given their longevity and capacity for learning, the reduced parental care observed today could be an adaptation to past interactions with humans.

Some historical accounts even suggest a higher level of parental investment in the past (Charruau et al., 2022).

Incubation and nest environment

The incubation period for American crocodiles has been reported to typically range from 80 to 90 days (Platt and Thorbjarnarson, 2000a). Duration of incubation is related to temperature (Mazzotti et al., 2022). Incubation temperatures in Florida and Haiti had ranges of 1.4°C and 0.9°C, respectively (Thorbjarnarson, 1988; Mazzotti et al., 2022), with maximum temperatures being reached at night due to thermal buffering properties of the soil. Mean incubation temperatures have been shown to increase over the time; in Florida, mean incubation temperature increased from 30.9°C in late May – early June, to 34.3°C in early August. Mean nest temperature is correlated with mean air temperature (Lutz and Dunbar-Cooper, 1984).

Gas exchange characteristics of nests are influenced by soil type, which affects the properties of oxygen diffusion, water content and particle size (Lutz and Dunbar-Cooper, 1984). Variations in these factors demonstrated an increase in partial pressure of carbon dioxide (PCO_2), and a decrease in partial pressure of oxygen (PO_2) during incubation. Soils with much finer particle size demonstrated a lower potential for gas diffusion, a lower PO_2 and higher PCO_2. Under normal conditions egg mass shows a decrease (water content) of 8.6% - 15% during incubation (Lutz and Dunbar-Cooper, 1984).

Clutch size of American crocodile eggs ranges from 22 to 105 (Platt and Thorbjarnarson, 2000a; González-Desales et al., 2016; Mazzotti et al., 2022). Very high clutch sizes may be the result of more than one female ovipositing in a single nest. Evidence supports this, as in Florida and Haiti two clutches laid by different females were laid in the same nest (Lutz and Dunbar-Cooper, 1984; Thorbjarnarson, 1988). According to Platt and Thorbjarnarson (2000a) a single clutch usually contains 30 – 60 eggs. Egg hatching success is affected by fertility rates and environmental factors, flooding, desiccation, and predation. Egg fertility rates were investigated in Florida and Haiti by looking for the presence of banded and unbanded eggs near the end of the incubation period (Lutz and Dunbar-Cooper, 1984; Thorbjarnarson, 1988). Fertility rates (banding present) of individual nests ranged from 46 – 100% (Kushlan and Mazzotti, 1986). On average, only 9.9 – 10% of eggs were unbanded (infertile). An increase in soil moisture reduces soil oxygen diffusion capacity, as well as that of the eggshell. Flooding results in drowning of embryos within eggs. American crocodile nest in the dry season, and nests are constructed in low lying areas. Subterranean flooding appears to affect hole nests to a greater degree than mound nests (Mazzotti et al., 2022). Nesting sites with better drainage and a higher elevation are at a lower risk of flooding.

Predation of nests is variable depending on the nesting site and the predators in the area (Platt and Thorbjarnarson, 2000a; González-Desales et al., 2016). The actual estimates of the impact of

predation on nests is not well quantified. Raccoons (*Procyon lotor*) have been observed predating American crocodile nests where their ranges overlap. Green iguanas *(Iguana iguana*) have been recorded inadvertently digging up crocodile eggs when nesting in crocodile nests themselves (Platt and Thorbjarnarson, 2000a; Platt et al., 2010). Mammals appear to be the most frequent predators of nests; in Florida, raccoon predation rates have declined likely due to the reduction in the raccoon population (Mazzotti et al., 2022). Platt et al. 2014 reported American crocodile eggs being predated by Black Vultures (*Coragyps atratus*) and Turkey vultures (*Cathartes aura*) in the Punta Sur Ecological Park, Quintana Roo, Mexico, and while this has not been observed infrequently oophagy has likely gone unnoticed and more widespread than publications suggest.

Diet and feeding

Similar to most crocodilians, *C. acutus* is a dietary generalist that consumes a wide variety of prey such as invertebrates, amphibians, reptiles, birds and mammals (Platt et al., 2013; Balaguera-Reina et al., 2018). In offshore marine habitats of Belize, Mexico (Quintana Roo), and Panama, the diet consists largely of marine invertebrates, particularly various species of crabs, gastropods, and bivalves (Villegas and Schmitter-Soto, 2008). Fruit and vegetation are occasionally consumed by *C. acutus*, although the dietary significance of frugivory is poorly understood (Platt et al., 2013; Platt et al., 2014; González-Solórzano et al., 2016). *C. acutus* exhibits the typical ontogenetic dietary shift with smaller size-classes consuming mostly invertebrates and larger individuals taking increasing amounts of vertebrate prey (Balaguera-Reina et al., 2018). The variety in diet strongly correlates with the size of the crocodile. Hatchlings and juveniles exhibit a wide range of prey species, with the common factor being the size of the prey (primarily consuming aquatic and terrestrial invertebrates or small fish). Prey reported from hatchlings include fiddler crabs, Hymenoptera, and amphipods (Balaguera-Reina et al., 2018). Juveniles have been observed preying on fiddler crabs of the genus *Uca*, Odonata larvae, and Coleoptera. Other prey items include Arachnida, Lepidoptera, Scolopendia, and Gerridae (Platt et al., 2013; Balaguera-Reina et al., 2018). Fish constitute a minor portion of the diet for both juveniles and hatchlings (<0.9 Total length (TL)), accounting for 9.3%. Sub-adults typically consume insects, fish, frogs, small turtles, birds, and small mammals. Adult crocodiles primarily feed on fish, although turtles and domestic animals (such as dogs, cats, and goats) are also commonly preyed upon (Platt et al., 2013; Balaguera-Reina et al., 2018).

Feeding behaviour is both passive and active. Juveniles are frequently seen at night along shallow water shorelines, remaining stationary and side swiping their jaws at surface disturbances (Villegas and Schmitter-Soto, 2008). Adult crocodiles are frequently observed in shallow water areas with high concentrations off cichlids. Some crocodiles remain submerged on the bottom, side swiping at passing fish. Crocodiles are observed concentrating under heron rookeries during nesting, likely waiting to catch young falling from the nest (Thorbjarnarson, 1989).

Lifespan

The lifespan of American crocodiles is not well known, due to their inconspicuous nature and difficulty in determining age in crocodilians (Grigg and Kirshner, 2015; Wilkinson et al., 2016). However, the lifespan of *C. acutus* is estimated to be between 60-70 years in the wild and 45 years in captivity (Briggs-Gonzalez et al., 2017)

Human-crocodile interactions

Human crocodile conflict (HCC) is on the rise in areas where the crocodile populations have become more abundant in recent years (García-Grajales and Buenrostro-Silva, 2019); Puerto Vallarta, lázaro Cárdenus and Pinotepa Nacional were identified as high-risk areas. An initiative from the Mexican Government through the National Environmental Agency (SEMARNAT) called “SOS crocodile” has identified a team in each region of the country to respond to incidents of human-crocodile conflict, gather information on the event, and take action to mitigate the problem. This pattern of increasing crocodile populations in areas of increasing human development are likely to result in an increase in incidents without the implementation of effective management and education programmes (García-Grajales and Buenrostro-Silva, 2019).

In Colombia, negative human-crocodile interactions are recorded as increasing in frequency and negative outcomes (crocodiles killed). Balaguera-Reina and Farfàn-Ardila (2018) reported three fatal incidents caused by *C. acutus;* They identified a significant gap in public understanding, particularly evident in media coverage, which undermines the efficacy of implementing robust management strategies. Failure to address this knowledge deficit and reshape local perceptions of *C. acutus* could lead to a surge in adverse encounters as the crocodile population grows.

Pooley et al., (2021) surveyed 23 countries across Latin American, to identify trends in negative human-crocodile interactions. They found 74% of the countries reported negative interactions increasing or unchanged, 39% experienced an upward trend. The major cause for killing crocodiles were reported as retaliation or fear from crocodile attacks on humans, livestock and pets. Only eight of the countries had management policies in place to handle human-crocodile interactions.

Conservation activities play a crucial role in stabilising and expanding the depleted range of *C. acutus* in numerous countries (Pooley et al., 2021). However, without the implementation of effective policies and the initiation of educational initiatives for local communities, which are likely to experience heightened human-crocodile interactions (Balaguera-Reina and Farfàn-Ardila, 2018), there is a risk of a shift in attitudes towards the conservation of *C. acutus*. Failure to address these concerns could potentially undo much of the progress that has been made (Corvera, Manalo and Aquino, 2017; García-Grajales and Buenrostro-Silva, 2019).

Conservation and threats

Once heavily hunted for its hides until protection measures were implemented in the 1970s, *C. actus* continues to face threats such as illegal hunting and habitat degradation due to coastal development (Thorbjarnarson, 2010; Rainwater et al., 2019). In addition, overharvesting of fish in the Dominican Republic and predation on young individuals by various species further contribute to population declines (Greco Jr. et al., 2023). While the species is showing signs of recovery in many areas of its historic range, certain regions such as Colombia and Ecuador still face challenges (Carvajal, Saavedra and Alava, 2005; Balaguera-Reina and Farfàn-Ardila, 2018). Although most range states have management measures in place, enforcement against illegal hunting remains lacking (Thorbjarnarson et al., 2006). Conservation efforts include protected areas, sanctuaries, captive breeding programs, and commercial farming operations. Urgent conservation priorities include surveys in the Guayas River system in Ecuador and the Tumbes area in Peru to assess population status and genetic distinctiveness (Rainwater et al., 2019, 2021), along with attention to the Magdalena/Cauca River basin in Colombia (Balaguera-Reina, Venegas-Anaya and Densmore, 2014) and the development of a conservation program in Jamaica (Henriques, Wilson and Ross, 2012).

In addition to the high-priority conservation efforts, moderate-priority actions include genetic evaluations of the American crocodile due to its wide-ranging nature, potential hybridisation with other species of crocodilian (*C. moreletii* and *C. rhombifer*) (Hekkala et al., 2015; Milián-García et al., 2015; Wilkie et al., 2024), necessitating further investigation into the evolutionary implications of such interactions. Moreover, assessing the population status of *C. acutus* in regions like the Cayman Islands, El Salvador, Guatemala, and Haiti is considered crucial, given the lack of recent information, to develop appropriate conservation and management plans based on population numbers, habitat availability, and existing threats (Thorbjarnarson, 1988; Escobedo-Galván, 2004; Thorbjarnarson et al., 2006). Further investigations into the ecology and population biology of American crocodiles, particularly in less-studied regions, are also recommended to enhance overall species management, addressing aspects such as genetic diversity, movement patterns, habitat use, and behaviour, which can aid decision-makers dealing with human-crocodile conflict (Platt and Thorbjarnarson, 2000b; Villarroel et al., 2005; Charruau et al., 2010; Milián-García et al., 2015).

In Belize, the American crocodile population had shown signs of recovery along the cayes and atolls within the coastal zone (Platt and Thorbjarnarson, 2000b). In 2008 the population in Turneffe atoll exhibited a possible decline (Rainwater and Platt, 2009), but subsequent surveys over the following four years indicated this to be seasonal variation in nesting activity and encounter rates, and populations appeared to be stable (Rainwater, 2013; Platt and Rainwater, 2014) . The primary conservation threat to *C. acutus* in Turneffe atoll and throughout the coastal zone of Belize continues to be the loss of habitat, especially critical nesting beaches, due to human development (Rainwater

and Platt, 2009; Rainwater, 2013; Platt and Rainwater, 2014). Genetic studies appear to have shown that the only remaining non hybrids are found along the insular caye and atoll populations in Belize (Hekkala et al., 2015; Wilkie et al., 2024).

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Chapter 2

Description of the study site

General overview of Ambergris caye

Belize is a small country measuring just 22,970 km^2 and sharing borders with Mexico to the north, Guatemala to the west and south and the Caribbean Sea to the east (see Figure. 2.1). Its population in 2010 was 312,971, making it the least populated and the least densely populated country in the Central American region (Belize Census 2010).

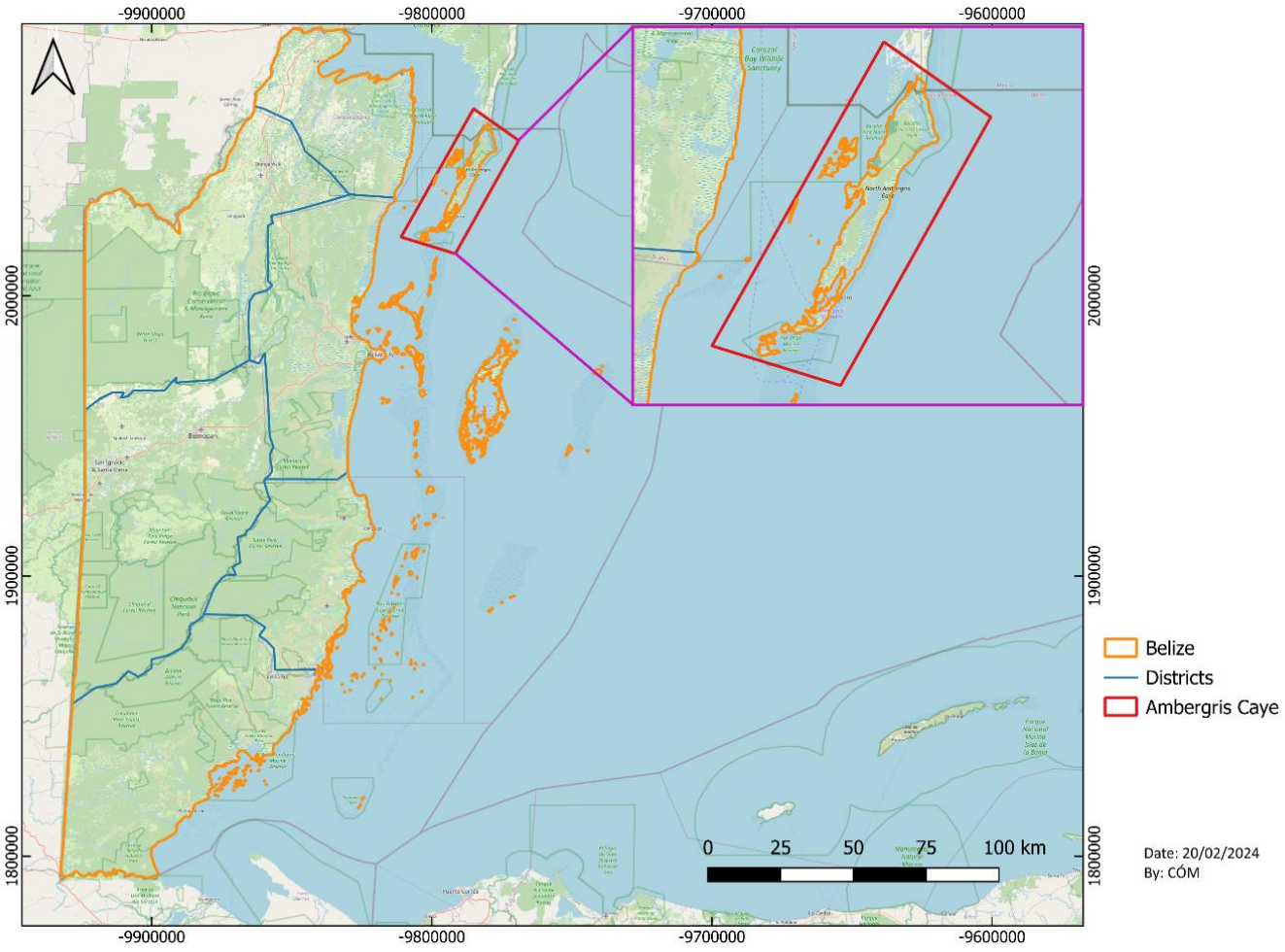

Figure 2.1. Regional map of Belize and Ambergris caye study site. Map generated using QGIS.

Ambergris caye, the largest island of Belize, is a long narrow island located north-east of the mainland in the Caribbean Sea with approximate coordinates of 18 00'N and 87 94'W (see Figures 2.1 and 2.2). It is approximately 40 kilometres long from north to south and 1.6 kilometres wide giving a total surface area of approximately 64 km^2. The island, like many Caribbean islands, has a geological history shaped by the accumulation of coral reef structures (Mazzullo, 2006). Over millions of years, the remains of marine animals such as corals, molluscs, and other calcareous organisms contributed to the formation of the island. The limestone bedrock, which constitutes the bulk of the island, is a result of the gradual deposition and compression of these organic remains. Ambergris caye has a unique ecosystem compared to mainland Belize. It is characterised by its coastal mangrove swamps, lagoons and diverse ecosystems, with mangrove and littoral forest

dominating the caye. Littoral forests are located on narrow coastal strips of sand dunes. These forests are sparse on the mainland and have historically been converted into coconut plantations (Mayfield & Simmons, 2019). Currently they are being transformed for tourist and residential development. In areas that experience frequent tidal flooding, *Rhizophora mangle* predominates. Where salinity is between 30-50% or when the area is disturbed *Avicenna germinans* dominates.

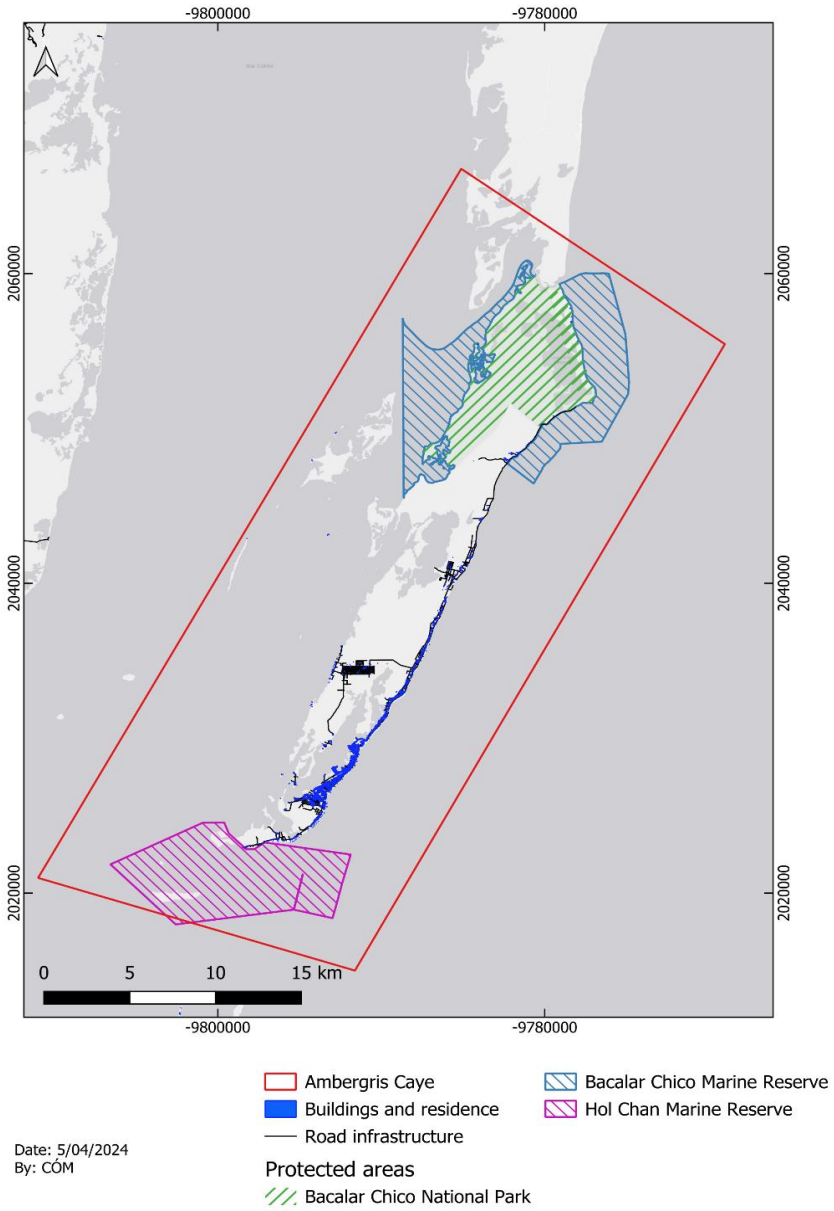

Figure 2.2. Map of Ambergris caye, Belize. With protected areas and buildings, residence, and road infrastructure. Map generated using QGIS.

The world's second longest barrier reef, the Belize Barrier Reef (BBR), part of the Great Mayan Reef, runs parallel to the Ambergris caye's eastern coast and contributes to its unique geographical features (Macphail et al., 2017). The Belize Barrier Reef, at 250 kilometres long, is the largest reef complex in the Atlantic and extends from the Yucatan Peninsula to the Gulf of Honduras (James and Ginsburg, 1979; Gischler and Hudson, 2004). In addition to the islands or 'Cayes' along the reef edge, of which Ambergris caye is the largest atoll, the complex includes Glover's Reef, Lighthouse Reef and Turneffe atoll. The BBR runs in a north-east direction, paralleling Belize's Caribbean coastline, and marks the rim of a carbonate platform or shelf, although the 'barrier' reef becomes a 'fringing' reef in northern Belize and adjoining Yucatan (James and Ginsburg, 1979; Gischler and Hudson, 2004). A total of 65 coral species has been identified in the reef (Alves et al., 2022). The BBR was established from >8.26 to 6.68 ky BP ("thousands of years Before Present") on Pleistocene reef limestones (Gischler and Hudson, 2004). The elevation of the Pleistocene limestone that underlies the majority of the reef varies from about 1 metre above sea level on Ambergris caye in the north to >25 metres below sea level at the southern end (Purdy, 1974).

Ambergris caye is unique among the atolls of Belize in that it is only separated from the Mexican mainland by a narrow marine channel possibly carved out by the ancient Mayan race (Author and Guderjan, 2004). On the Belize side of this border, situated at the northernmost tip of Ambergris caye, including the northern section of the Belize Barrier Reef System, is found the Bacalar Chico Marine Reserve and National Park (BCMRNP) (see Figure. 2.2), one of seven marine protected areas that form the Belize Barrier Reef World Heritage Site. This area covers 60 km^2 and approximately 15,350 acres of diverse marine habitat, encompassing coral reefs, seagrass beds, mangroves and coastal lagoons. A protected area since 1996, BCMRNP shares its northern border with Arrecife de Xcalak, a marine protected area in southern Mexico (Rivera, 2002; Cabanillas-Terán et al., 2019). Noted for its rich biodiversity, the area is home to a number of ecologically and commercially valuable species (Cabanillas-Terán et al., 2019).

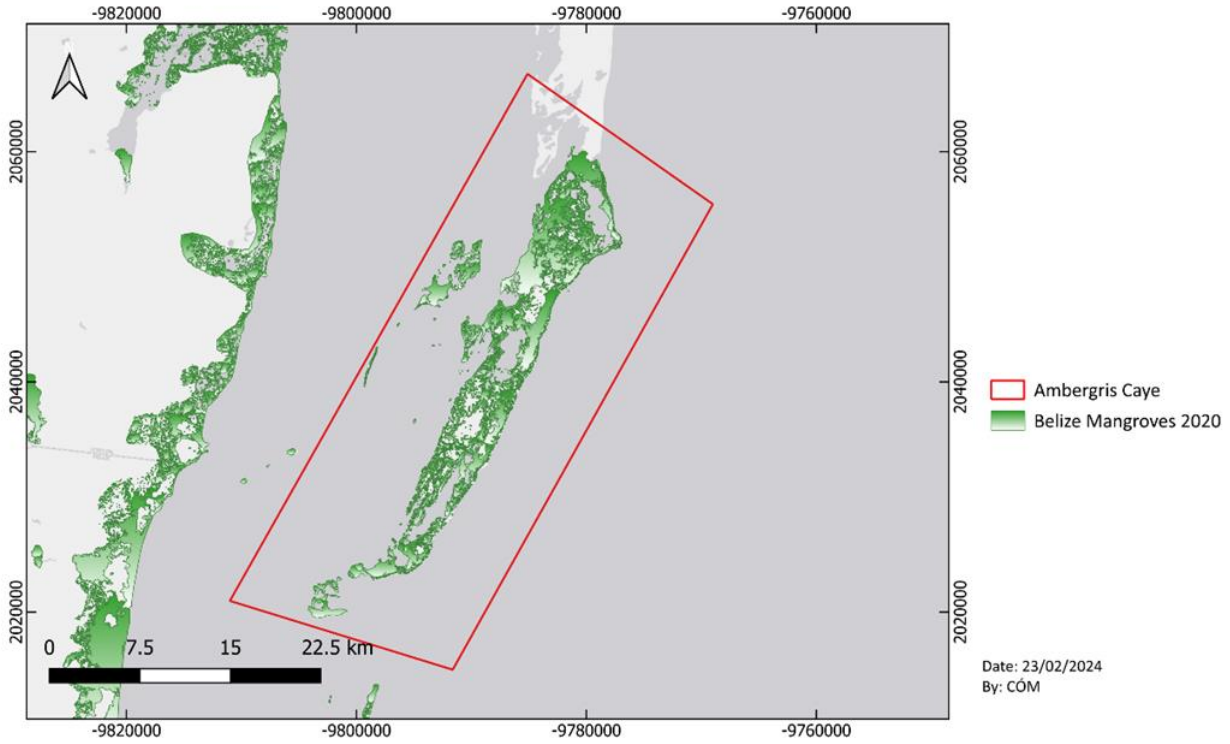

Figure 2.3. Map of Landsat imaging of mangrove cover density in Belize adapted from data collected from Alves et al., (2022) Map generated using QGIS.

Ecosystems of Ambergris caye

Nearly half (47.6%) of Ambergris caye is covered by mangroves (see Figure 2.3), while bodies of water account for 26% of the area. Four species of mangrove tree have been documented on the island: They are the red mangrove (*Rhizophora mangle*), the black mangrove (*Avicennia germinans*), the white mangrove (*Laguncularia racemosa*), and the buttonwood (*Conocarpus erectus*) (Alves et al., 2022). The red mangrove is most often found along edges closest to water and is easily identified by its network of aerial prop roots which are used to support the plant. Red mangroves can attain heights of 25 to 38 metres but average 8 to 10 metres on most shorelines. They regularly appear as smaller trees in marginal habitats. The black mangrove has a distinctive horizontal cable root system that radiates out from the tree, and these are usually found further away from the water's edge. The trees can be recognised by the small protrusions called pneumatophores that extend 2 to 20 cm above the substrate and encircle the base of the tree. The white mangrove and the buttonwood species are generally located further away again from the water's edge and deeper into the interior as they can grow in areas with low tidal wave activity. White mangroves can grow in either tree or shrub form and can reach heights of up to 15 metres or more. Some white mangroves form erect, blunt-tipped, pneumatophores if growing in anaerobic or chemically stressed soils. Buttonwoods can also appear in tree or shrub form and can reach heights of 12 to 14 metres (Ball, 1996; Rhine et al., 2013).

Buttonwoods are able to grow in areas seldom affected by tidal waters. The micro roots stabilise silts and sands maintaining water clarity and quality (Snedaker, 1982).

Lowland broad-leaved dry forest is a very distinctive forest type, confined in Belize to dry, shallow soils found in the Bacalar Chico National Park and Shipstern Native Reserve area in eastern Corozal district. It has a low canopy (7-8m) and trees are generally of narrow girth, resulting in a forest with a "scrubby" appearance (Meerman and Sabido, 2001). To the west of the caye is the shallow Corozal bay that is dominated by seagrass, primarily *Thalassia testudinum,* a critical food source for the West Indian Manatees found along the caye (Murphy et al., 2022). See Figure 2.4 for a map of the various ecosystems of Belize.

The limestone landscape of BCMRNP gives rise to numerous creeks and lagoon systems, contributing to its rich biodiversity. The park hosts ecologically and commercially valuable species, making it a focal point for conservation efforts. However, the proximity of BCMRNP to the Belize Barrier Reef Reserve System has made Ambergris the most popular tourist destination and economic hub in all of Belize (Sweetman et al., 2019).

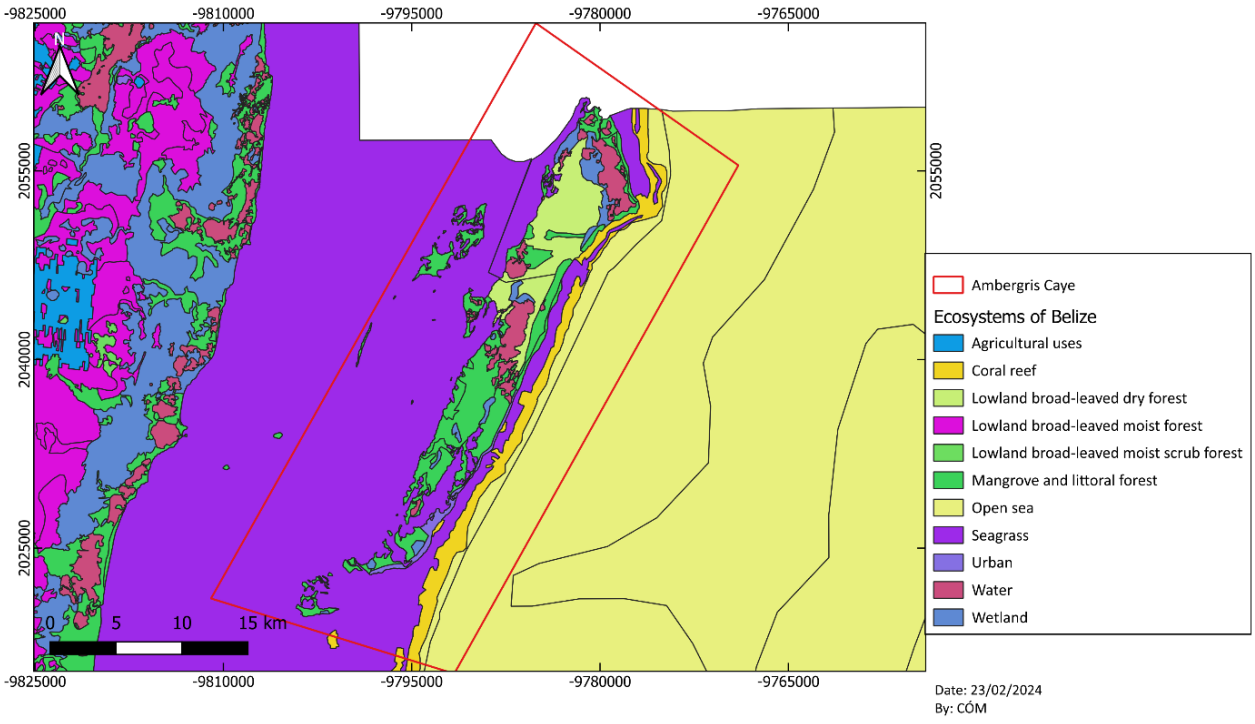

Figure 2.4. Map of the Ecosystems of Belize adapted from version 2017 Belize Ecosystems Map (Meerman & Sabido, 2001). Map generated using QGIS.

The region has undergone intense commercial and residential development along with significant population growth over the past two decades. It is susceptible to the impacts of tourism and commercial development, increasing pressure on its mangrove habitats (Sweetman et al., 2019) An understanding of the general trends in landscape dynamics is critical for the natural resource-based tourism industry in Belize to thrive. To estimate loss in vegetation cover and increases in urban and barren land, Sweetman et al. (2019) used Landsat satellite imagery to document vegetation cover change on Ambergris caye, Belize, from 2000 to 2017. The results indicated a 10.85% decrease in vegetation and a 39% increase in urban and barren land during a seventeen-year study period with an attendant annual forest loss rate of 0.67%. Threats come from many sources including increased tourism, rapid coastal development, pollution, improper waste management, and ineffective institutional and legal frameworks.

The recent construction of eleven hotels and other major infrastructure for tourism as well as attendant residential property is putting pressure on the mangrove habitats. This destruction may also have a serious impact on the hundreds of species that live in the arboreal, sub-tidal, inter-tidal, and benthic communities associated with these forests. Increased tourism will lead to more facilities andbuildings, and these will need to be serviced by roads and modes of transport; this will inevitably lead to increased land clearance (Sweetman et al., 2019; Murray, 2021).

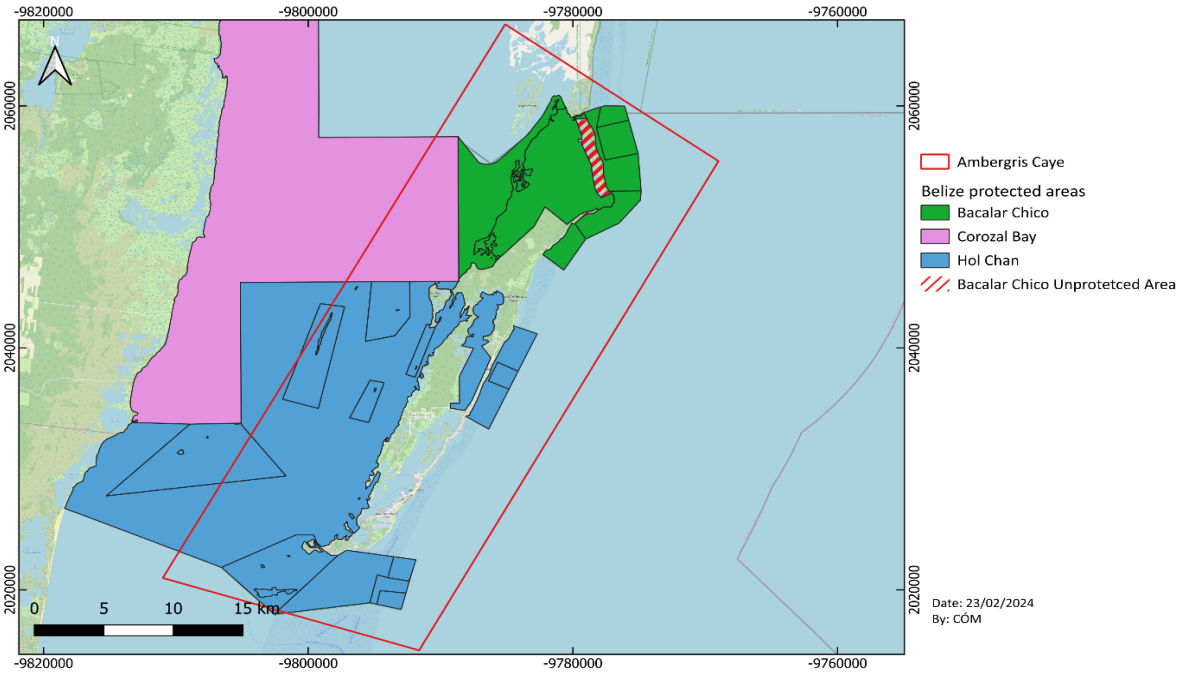

Figure 2.5. Protected sites within the Ambergris caye study site. Map generated using QGIS.

Protected areas in Ambergris caye

Currently 43% of Ambergris caye is classified as a protected area (see Figure. 2.5) (Sweetman et al., 2019). Hol Chan Marine Reserve, established in 1987 off the coast of Belize, adjacent to San Pedro on Ambergris caye, constitutes a significant marine protected area within the Belize Barrier Reef Reserve System, recognised as a UNESCO World Heritage Site. Encompassing an area of approximately 29 km^2, the reserve incorporates diverse marine ecosystems, including seagrass beds, coral reefs, and mangrove forests (described above).

Of particular importance within Hol Chan is Shark Ray Alley, a site with notable snorkelling and diving significance. Originally a locale for traditional fishing activities, the area has evolved into a notable attraction where the presence of nurse sharks (*Ginglymostoma cirratum*) and stingrays (*Hypanus americanus* and *Urobatis jamaicensis)* has been established through the historical cleaning of fishing catches by local fishermen. This phenomenon has given rise to opportunities for eco-tourism, allowing observers to witness these marine species in their natural habitat (Murray, 2021).

The reserve is strategically divided into four zones, each serving distinct purposes, including zones for sustainable fishing practices, general use areas, and a no-take zone designed to preserve critical habitats and facilitate the recovery of marine populations. Hol Chan Marine Reserve assumes a pivotal role in marine conservation endeavours, providing sanctuary to diverse marine species such as corals, fish, sea turtles, and manatees (Gibson et al., 2004).

Corozal Bay Wildlife Sanctuary (CBWS), established in 1998, covering approximately 720 km^2. Governed by the National Park Systems Act of 1981 and integrated into Belize's National Protected Areas System, CBWS operates as a transboundary protected area, forming a binational partnership with Mexico's Sanctuario del Manati. As part of the Northern Belize Coastal Complex (NBCC), CBWS functions within a river-to-reef seascape, serving as a crucial sediment and contaminant settling basin, safeguarding the health of the Mesoamerican reef system.

CBWS boasts a diverse ecosystem, housing stable manatee populations, vital bird nesting sites, Belize's sole recorded bull shark nursery, extensive coastal and caye mangroves, and the exclusive stromatolite reef system (Lohberger et al., 2019). The sanctuary plays a pivotal role in transboundary estuarine conservation, fostering collaboration between Belize's Southern Environmental Association (SEA) and its Mexican counterpart, IBANQROO, to enhance conservation outcomes on both sides of the border. The sanctuary's significance extends to sustaining the livelihoods of coastal communities, particularly Sarteneja village, reliant on CBWS marine resources.

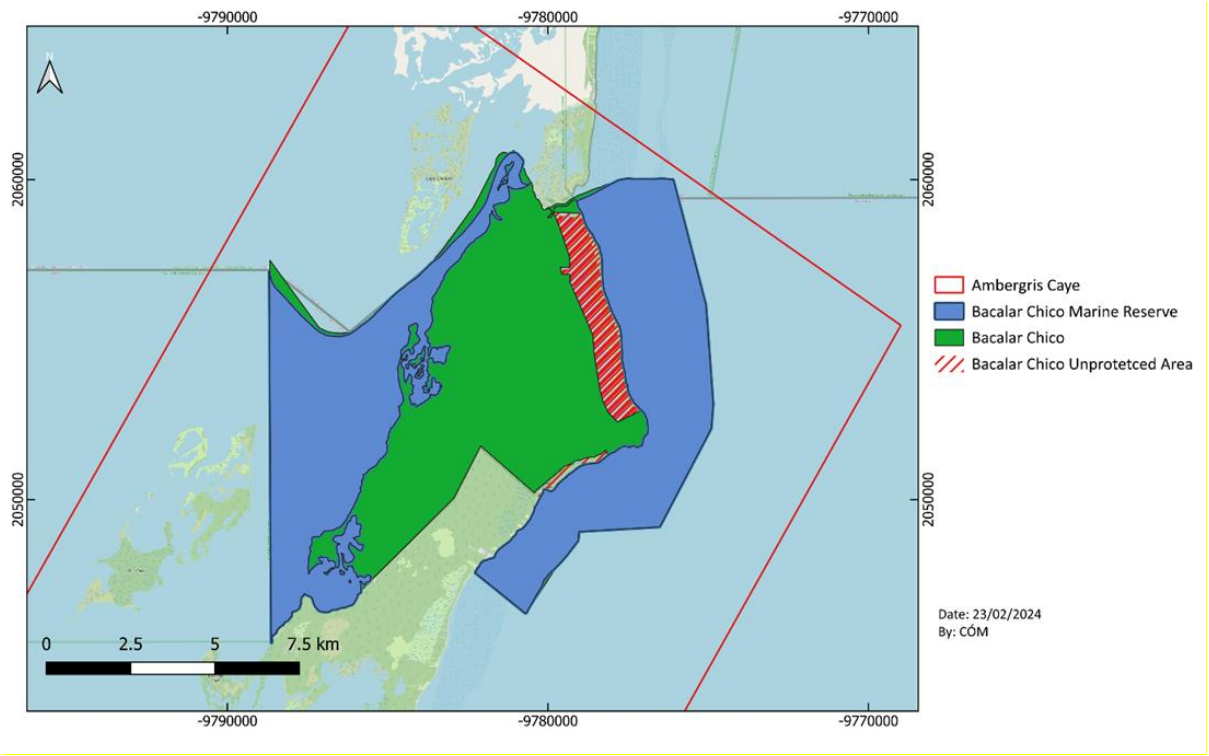

Figure 2.6. Bacalar Chico National Park and Marine Reserve. Map generated using QGIS.

Bacalar Chico Marine Reserve and National Park (BCMRNP) (see Figure. 2.6), established in 1996, stands as a significant conservation stronghold in Belize, located on the northern expanse of Ambergris caye. Covering an expansive 28,169 acres, this protected area, governed by Belize's National Parks System Act of 1981, plays a pivotal role in Belize's National Protected Areas System. Its distinction extends to being part of the UNESCO World Heritage Site, designated in 1996, within the Belize Barrier Reef Reserve System (Gibson et al., 2004).

BCMRNP is considered to be ecologically significant, spanning diverse landscapes from Chetumal Bay to the Caribbean Sea (Chapman, 2012). The reserve encompasses 12,640 acres of terrestrial habitat, including the Bacalar Lagoon, and a 15,529-acre marine reserve, contributing to the broader Mesoamerican Barrier Reef System. Notably, BCMRNP serves as a haven for varied marine species, sustaining a balanced fishing zone that supports local communities. Beyond its ecological importance, the reserve boasts ancient Mayan archaeological sites, of historical and cultural value.

However, BCMRNP has faced challenges (Dahlgren, 2009). News reports in October 2007 suggested potential de-reservation, allowing for the purchase of 2700-acre area along the eastern beachfront by private investors. While details on the 2700-acre de-reservation area remain unclear, this event raises concerns about its impact on the reserve's conservation status. Co-managed by Belize's Ministry of Agriculture, Fisheries, Forestry, The Environment, and Sustainable Development, BCMRNP

objectives are ensuring fishery health, regulating water sports, conducting research, providing employment opportunities, and curbing illegal activities harmful to its unique flora and fauna.

Biodiversity of Ambergris caye

Ambergris caye is home to a much greater biodiversity in both marine and terrestrial flora and fauna when compared to its neighbouring islands, such as Turneffe atoll and Caye Caulker (Chapman, 2012; Platt et al., 1998, 2000, 2002). Factors which influence this may include the island's proximity to the Yucatan peninsula in Mexico, its larger size and the presence of the BCMRNP. Ambergris caye is separated from the Mexican mainland by the narrow Boca Channel, an interesting question arises as to whether there is any evolutionary distinction between the mammalian species between the Quintana Roo northern Mexico side and the southern Ambergris caye side. However, very little research has been carried out in this area. While there are confirmed sightings of large apex predators such as jaguar (*Panthera onca*), puma (*Puma concolor*), ocelots (*Leopardus pardalis*) as well as prey species such as collared peccary (*Dicotyles tajacu*), white-tail deer (*Odocoileus virginianus*), and coatimundi (*Nasua nasua*), there is little known about the population dynamics of the species and the level of movement between populations on both sides of the channel (Chapman, 2012). However, as the channel is only 5 metres wide in places, it can be assumed that larger species are capable of swimming across the narrow channel, while smaller species may be limited to one side (Palafox et al., 2022).

Ambergris caye, like neighbouring Yucatan, is home to a large range of herpetofauna diversity. Ophidians, such as boa constrictors (*Boa imperator*), Mexican parrot snakes (*Leptophis mexicanus*), and fer de lance (*Bothrops asper*) snakes are present. Saurians, such as black iguana (*Ctenosaura similis*), basilisk (*Basiliscus vittatus*), and many species of anoles.. There are two species of crocodilian found in Belize and the wider Yucatan, the Morelet's crocodile (*Crocodylus moreletii*) and the American crocodile (*Crocodylus acutus*) (Chapman, 2012). Only the latter species, the American crocodile, is found on Ambergris caye (Chenot-Rose, 2013). American crocodiles are listed under CITES Appendix 1 and classified as Vulnerable by the IUCN in Belize. Legal protection was afforded to both species under the Wildlife Protection Act of 1981 (Marin, 1981), and surveys conducted by Platt and Thorbjarnarson, (2000) from 1992 - 1997 suggest *C. moreletii* populations are recovering.

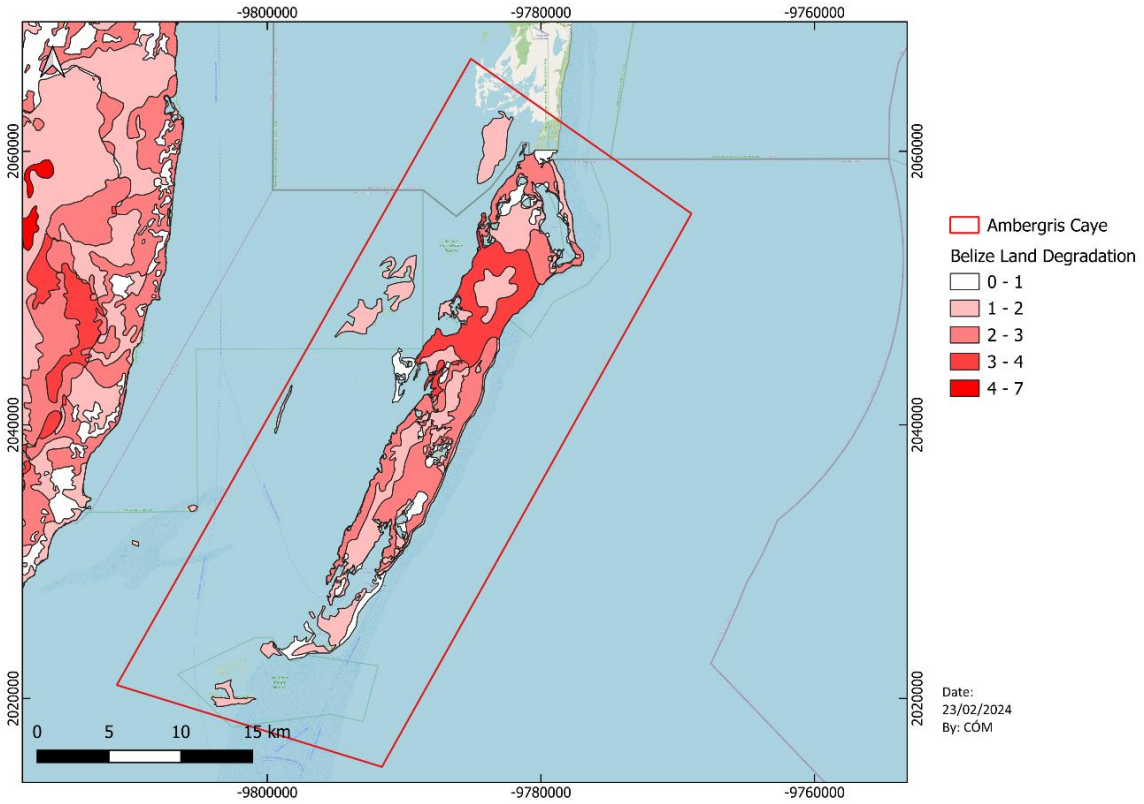

Figure 2.7. Levels of land degradation adapted from (Meerman and Cherrington, 2005). 0-4 (low), 5 (medium), 5-7 (High). Map generated using QGIS.

Human population and demography

With a population of 13,380 (Belize census, 2010) recorded in the last census conducted in 2010 and an estimated current population of over 18,000, Ambergris caye is now, one of the most densely populated areas in Belize. A population density of 286 people per km^2 and rising, may have negative implications for wildlife (Sweetman et al., 2019). The population density, however, is unevenly distributed across the island with 11,765 or 87% residents concentrated in the San Pedro Town area on the south of the island. The remainder of the population are scattered across a number of small villages, many of them serving the islands growing tourism industry. Because of the island's small size, the main form of transportation is the golf cart.

With the exception of San Pedro Town, there is a lack of sewage treatment facilities on the island (Grau et al., 2013). There is evidence that improper waste disposal is having a negative impact on the environment and mangrove habitats in particular. Even in San Pedro Town, the sewage treatment plant is considered to be ineffective, expensive, and limited to households in the core area of the town (Grau et al., 2013). The majority of San Pedro Town residents are not connected to the system but instead, rely on pit latrines and septic systems. The caye has experienced significant commercial and residential expansion alongside a rapid surge in population over the last two decades (refer to Figure

2.7). Particularly, the previously minimally developed northern section of the island has undergone substantial degradation as the population expands outward (Sweetman et al., 2019).

Tourism is beneficial for the economy and brings much needed opportunities and employment. However, it needs to be well managed and controlled to avoid unnecessary destruction (Sweetman et al., 2019). The residents of Ambergris caye must thoughtfully consider the direction of its development, ensuring that the preservation of its exceptional environment remains a top priority. The high intensity of future developments in the fishing and tourism industries threatens the caye's ecology through uncontrolled expansion and exhaustion of resources (Rivera, 2002; Sweetman et al., 2019). Like so many countries, laws exist that can potentially protect the environment and in Ambergris caye the mangrove habitats, but enforcement of these laws is often lacking (Young, 2008).

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Chapter 3

American crocodile, *Crocodylus acutus*, population assessment in Ambergris caye, Belize, Central America

Abstract

Surveys of the American crocodile (*Crocodylus acutus*) in Belize over the last few decades have yielded conflicting evidence on the stability of the population along the country's cayes and atolls. These areas along the coast of Belize are considered to be a stronghold for *C. acutus* in the country. The main threats facing the population in these areas are habitat loss, primarily due to human development and the loss of nesting sites. This study, conducted between May-September 2023, used a combination of nocturnal spotlight surveys and nest counts to evaluate the current status of *C. acutus* populations in Ambergris Caye. A total of 19 surveys nocturnal spotlight surveys were conducted at unique locations. Spotlight surveys were conducted from a 19.6 ft Carolina Skiff with a 40 hp Yamaha four stroke outboard as well as Club Cart CarryAll 1500 UTV, beginning 10 to 30 minutes after sunset. The average speed by both skiff and cart was 2.5 km/hr. Surveyed areas included mangrove shorelines, canals, brackish water lagoons, waterways, and coastal beachfront, shoreline areas in Ambergris caye to reduce the level of error, in particular overcounting, each spotlight eyeshine was confirmed by two observers before it was documented.

A total of 199 *C. acutus* was observed along 171.5 km of the Ambergris caye coastline, lagoons and wetlands, with an overall encounter rate of 1.16 crocodiles/km. This encounter rate was higher than that reported for surveys conducted in 2010/11. Out of the 199 crocodiles encountered and based on total length,22% were adults, 10% sub-adults, 16% juveniles, 22% yearlings/hatchlings and 30% were individuals whose size class could not be determined (eyeshine only). Nine nests were found, five of which hatched and were located adjacent to the caye's sewage treatment ponds. The remaining four nests were located in highly developed and human-inhabited areas; one nest was destroyed by heavy machinery and another removed as it was located under a garbage "burn pit". Surveys of the Bacalar Chico National Park failed to find any evidence of nesting, but further nest surveys should be a high priority. Despite signs of a stable, if not slowly increasing, population present on Ambergris caye, the lack of critical nesting habitat with the primary nesting area being located adjacent to sewage ponds is a cause for concern. The heavily developed nature of the southern area of Ambergris caye has placed *C. acutus* populations in close proximity to humans and puts both at risk. Continued population assessments will be essential in monitoring the status of C. *acutus* in Ambergris caye, and management of the sewage ponds nesting beaches should be undertaken. Last, immediate management and conservation efforts should be made to further investigate the population status of crocodiles in Bacalar Chico National Park.

Introduction

To effectively study crocodilians for conservation management plans and ecological studies, it is essential to assess the population status of the species of interest in a given study area (Bayliss, 1987). Effective sampling of any species requires specialised techniques that suit the habitat and reflect the ecology of the target species (Cherkiss et al., 2009). Population studies of American crocodiles have used a range of techniques, including daylight ground counts (Nair et al., 2012), daytime aerial surveys (Combrink et al., 2012), and night spotlight surveys (Mauger et al., 2012). Recently, aerial drone surveys have emerged as a novel method in population studies for species such as *Crocodylus niloticus* and *Gavialis gangeticus*, among others. They offer a notably cost-effective approach to surveying river systems (Ezat, Fritsch and Downs, 2018; Platt et al., 2023; Sawan et al., 2023). However, the dense mangrove coverage and limited water visibility of the Ambergris caye habitat makes aerial surveying limited in its effectiveness (Bayliss, 1987; O'Brien, 1990).

The primary habitat of American crocodiles throughout Belize is heterogeneous, including mangrove wetlands and internal lagoons as well as coastlines of Belize's cayes and atolls. Most of the published literature for American crocodiles in Belize have involved studies within the mangrove wetland environment (Platt et al., 1999; Platt and Thorbjarnarson, 2000a;2000b; Platt et al., 2004; Rainwater and Platt, 2009; Chenot-Rose, 2013; Platt and Rainwater, 2014; Tellez, Boucher and Kohlman, 2016). Night spotlight surveys have been the preferred method of surveying, both in Belize and for crocodilians in general (Platt and Thorbjarnarson, 2000b; Rainwater and Platt, 2009; Combrink et al., 2012; Mauger et al., 2012; Chenot-Rose, 2013; Tellez, Boucher and Kohlman, 2016). Spotlight surveys rely on the reflective tapetum lucidum of the crocodilian eye, which reflects light ("eyeshine") when the animal's eyes are above water, allowing for the detection of animals at great distances and in situations where the animal might not have been otherwise seen (O'Brien, 1990). Spotlight surveys are considered very effective in providing the most reliable population data for crocodilians. As crocodilians of all sizes can be spotted using this technique, it also has the least likelihood of inherent bias towards a particular sex or size class (e.g. adults and sub-adults are much more visible during daylight surveys and aerial surveys).

Various factors, beyond population density, contribute to the count of crocodilians in a survey, and the complete crocodile population in a given area may not be entirely accounted for (Graham and Bell, 1969; Magnusson, Caughley and Grigg, 1978; Bayliss, 1987). Environmental variables such as wind, air and water temperature, and wave action introduce complexities that can influence survey outcomes and impact the visibility of animals (Woodward and Marion, 1979). Surveys employing two independent observers with lights enhance the chances of detecting overlooked crocodilians, particularly if one observer identifies an individual missed by the other (Lawson et al., 2022). This dual observation method helps bolster accuracy, as each sighting is confirmed by both observers.

(Magnusson, Caughley and Grigg, 1978; Bayliss, 1987). The cautious behaviour of crocodilians is an additional factor that can influence survey results (Lawson et al., 2022). This wariness can be gauged by the distance at which an observer can approach before the animals submerge (Webb and Messel, 1979; Pacheco, 1996). Assessing visibility across different habitats involves thorough daylight searches in a sample area following a standard survey.

Historically, American crocodiles have been surveyed intermittently in Belize since 1996-1997 up until 2016, with findings summarised in Table 3.1. These surveys predominantly targeted the atolls and cayes of Belize, recognised as strongholds for non-hybridised American crocodiles in the country (Hekkala et al., 2015; Wilkie et al., 2024), with Turneffe atoll identified as harbouring the most significant remaining insular population (Platt and Thorbjarnarson, 2000b). Currently, there are 4 crocodile conservation units "CCUs" in Belize (Turneffe atoll, Bahia de Chetumal, Gales Point and Lighthouse atoll). These areas are considered to be the most significant for the conservation of *C. acutus* in the country (Thorbjarnarson et al., 2006). The encounter rate of American crocodiles in Belize has consistently been relatively lower compared to other countries within their geographic range such as Costa Rica (Mauger et al., 2012) and Mexico (Charruau and Cedeño-Vázquez, 2005). Particularly concerning was the observed declining trend in encounter rate and nesting between 1996-2008 on Turneffe atoll (Rainwater and Platt, 2009); however, subsequent surveys over the following four years indicated this decline to be a reflection of seasonal variation in nesting activity and encounter rates, and the population overall appeared to be stable (Rainwater, 2013; Platt and Rainwater, 2014). Ambergris caye (see Figure. 3.1) underwent its initial American crocodile spotlight survey in 2010-2011 (Chenot-Rose, 2013), revealing a relatively high encounter rate compared to other areas within the Belize coastal zone. The current project aims to assess the population status of American crocodiles on Ambergris caye and if the population is facing pressures from opportunistic killing, accidental drowning in fishing nets, and habitat destruction, especially the development of critical nesting habitat (Rainwater and Platt, 2009), and to assess Ambergris caye's significance as a crucial stronghold for the species in Belize.

Table 3.1. Summary of historic population nocturnal eyeshine surveys of *Crocodylus acutus* in Belize.

Location	Year	Crocodiles	Distance (km)	Encounter rate (crocodiles/km)	Nests	Source
Turneffe atoll	1996-97	152	156.8	0.96	15	Platt and Thorbjarnarson, 2000
Cayes	1996-97	96	219.8	0.43	NA	Platt and Thorbjarnarson, 2000
Mainland	1996-97	14	576.6	0.02	NA	Platt and Thorbjarnarson, 2000
Lighthouse atoll	1996-97	1	NA	NA	1	Platt and Thorbjarnarson, 1999
Turneffe atoll	2002	49	40.1	1.2	8	Platt, et al., 2004
	2004	NA	NA	NA	20	Platt, et al., 2004
Turneffe atoll	May, 2008	23	46.6	0.49	0	Rainwater and Platt, 2009
	June/July 2008	8	45.3	0.18	2	Rainwater and Platt, 2009
Mean				0.34		
Ambergris caye	2010/2011	57	59.6	0.95	5	Chenot-Rose, 2013
Caye Caulker	2016	55	22.15	1.5	NA	Tellez, Boucher and Kohlman, 2016

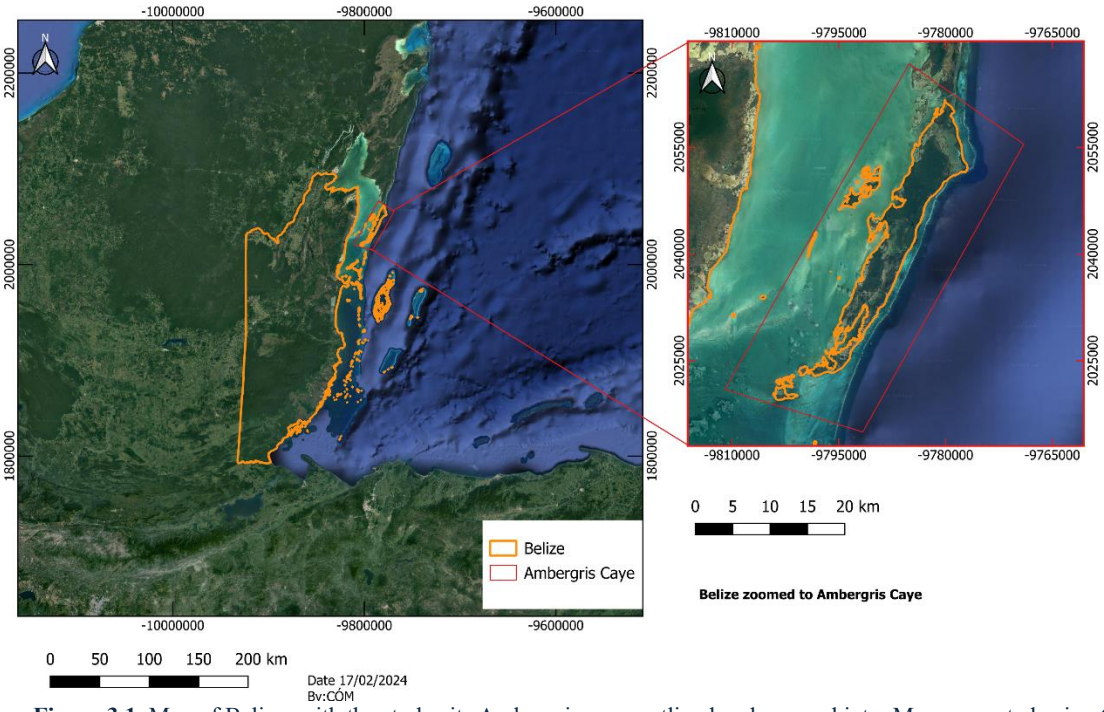

Figure 3.1. Map of Belize, with the study site Ambergris caye outlined and zoomed into. Map generated using QGIS.

The present investigation had the following objectives: (1) to estimate the size of the Ambergris caye American crocodile population, (2) to determine if the trend of the Ambergris caye American crocodile population is increasing, stable or decreasing (3) to identify crocodile nesting sites remaining on Ambergris caye, (4) to provide scientific data on crocodile status on Ambergris caye to the government of Belize to help inform the formation of a species conservation and management strategy.

Materials and methods

Fieldwork in Ambergris caye was conducted from 30 May to 31 August 2023. The crocodile population was counted using a combination of nocturnal spotlight surveys (Bayliss, 1987) and nest counts. Nocturnal spotlight surveys were conducted from water using a 19.6ft Carolina Skiff with a 40hp Yamaha four stroke outboard and from land using a Club Cart CarryAll 1500 UTV. Surveys began 10 to 30 minutes after sunset. The average speed by both skiff and cart was 2.5 km/hr. Surveyed areas included mangrove shorelines, canals, brackish water lagoons, waterways, and coastal beachfront, in Ambergris caye, south of Laguna de Cayo Frances to the southern-most tip of the island, Boca Chica and to the very Northern tip of the island, the boca channel and Laguna de Cantena in the BCMRNP area (see Figure 3.2).

Eyeshines of crocodiles were detected using Fenix TK16 flashlight with a max output of 3100 lumens, a Fenix HL60R headlamp with a max output of 950 lumens, and a LED Lenser H14R.2 headlamp with a max output of 1000 lumens. To reduce the level of error, in particular overcounting, each spotlight eyeshine was confirmed by two observers before it was documented (Magnusson, Caughley and Grigg, 1978, 1978; Lawson et al., 2022). Surveys were only conducted during times of optimal visibility and weather conditions. A total of 19 unique surveys, each conducted at a distinct location, were carried out (see Figure 3.2).. The beginning and endpoints of each survey route, and the distance traversed, was determined with a Garmin eTrex 20x handheld GPS.

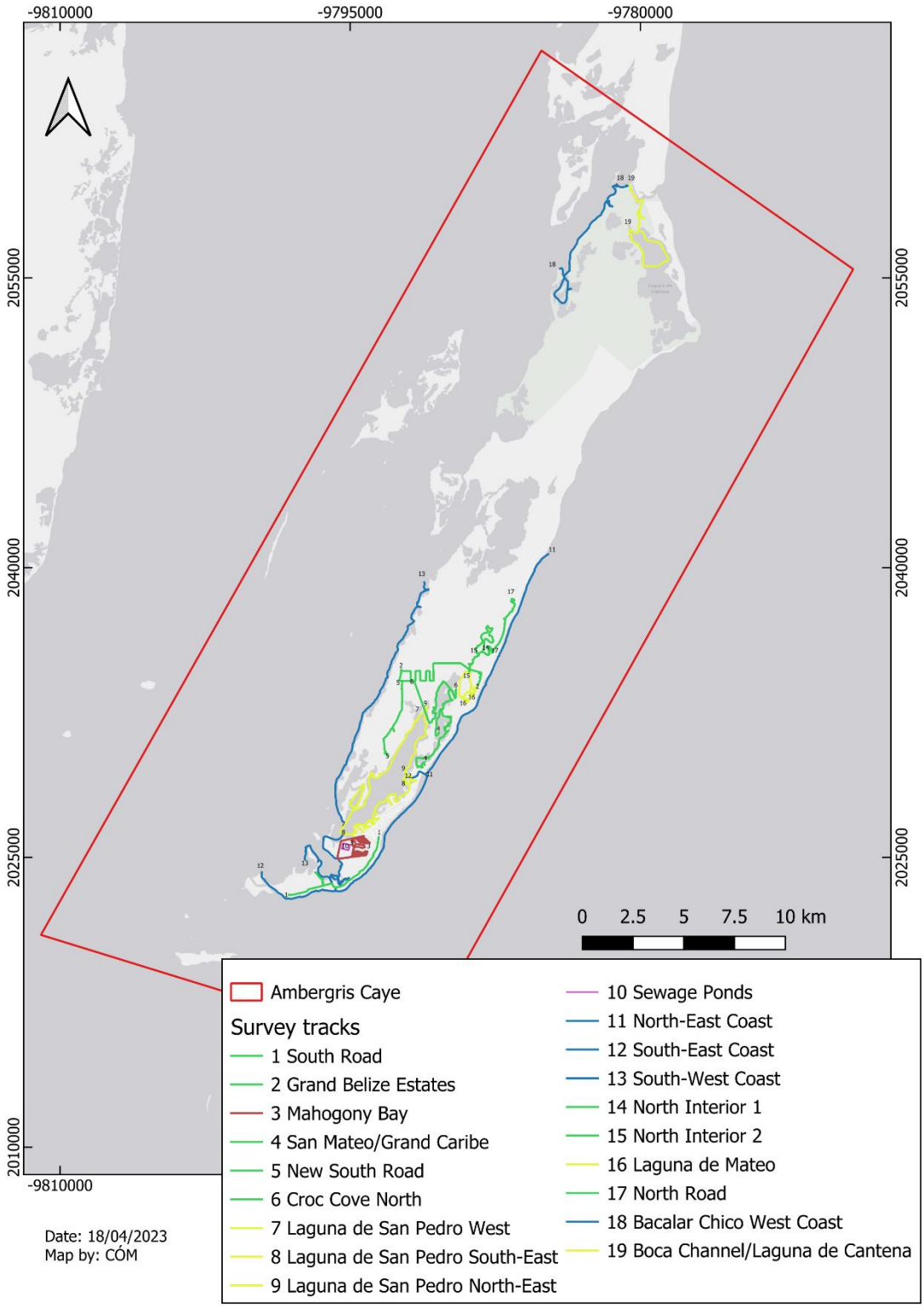

Figure 3.2. Locations of areas surveyed during nocturnal eyeshine surveys; colour coloured by habitat type (see main text) in Ambergris caye. Map generated using QGIS.

When a crocodile was spotted, it was approached slowly when possible, and GPS coordinates were recorded. When the animal could not be approached, GPS coordinates were recorded by the observer, and the distance of the animal from the observer was estimated as 0-5, >5-25, >25-50 and >50m. All crocodiles sighted were classified by an estimate of total length (TL), following the categorisation by Platt and Thorbjarnarson (2000b), Chenot-Rose (2013), and Tellez, Boucher and Kohlamn (2016), with hatchlings (TL<30 cm), yearlings (TL≤ 30 to 59 cm), juveniles (TL ≤ 60 to 119 cm), sub-adults (TL120 to 179 cm) and adults (TL>180 cm). Crocodiles that submerged before TL could be estimated were classified as "eyeshine only" (EO). Encounter rates were calculated as the number of crocodiles observed per kilometre of survey route (Bayliss, 1987; Platt and Thorbjarnarson, 2000b; Platt Rainwater and Nichols, 2004; Rainwater and Platt, 2009; Chenot-Rose, 2013).

Nests were located on foot by revisiting previous nest sites identified from historical nesting records (Chenot-Rose, 2013). In addition, and locations where newborn hatchlings were found during spotlight surveys were revisited and searched during the day in an attempt to find corresponding nests. were revisited and recently hatched nests were searched for during July 2023. The ACES Wildlife Rescue social media was used to learn of any previously unknown nesting areas by encouraging awareness in the local community of nesting and to encourage them to contact the NGO. In addition, a DJI Mavic pro drone was also used to investigate difficult to navigate terrain to search potentially suitable areas where nesting has yet to be documented. The drone was used under ideal conditions, overcast even lighting at a height of 60m and was flown regularly, especially in areas (beach ridges) where adults had been observed during night-time surveys. The GPS coordinates of each located nest were recorded. For each nest located, height, width, depth, substrate and distance from water were recorded.

Data analysis

Comparing current population to previous population assessment at Ambergris caye

To compare whether the encounter rate observed in the 2023 surveys was significantly different from the encounter rate observed in 2010-2011 (Chenot-Rose, 2013), a Wilcoxon rank sum test with a continuity correction was used comparing encounter rates of all surveys. The continuity correction was applied to address tied ranks in the data, ensuring the accuracy of the test statistic and the reliability of the results. In this comparison, the 2023 Bacalar Chico surveys were excluded from the analysis as this area was not surveyed in 2010-11.

Comparing crocodile encounter rates between habitat types

The study involved grouping encounter rate data by habitat types. Mangrove Wetland (8 surveys), Lagoon (5 surveys), Ocean (4 surveys), Canal (1 survey) and Sewage Pond (1 survey) were the habitat categories. The mean encounter rate values were calculated and subjected to a non-parametric Kruskal-Wallis test due to the non-normal distribution of the data.

Comparing crocodile encounter rates between Bacalar Chico and South Ambergris caye

Seventeen surveys were conducted in South Ambergris caye and 2 surveys were conducted in Bacalar Chico National Park. The mean values of encounter rates for each were calculated and subjected to a Wilcoxon rank-signed test comparing the encounter rates. All statistical analysis was carried out using RStudio version 4.3.2.

Nesting

The locations of nests in 2023 were compared with previous records.

Results

Table 3.2. Summary of nocturnal eyeshine surveys and encounter rates of *Crocodylus acutus*, 2023, Ambergris caye, Belize.

Location	Number of crocodiles	Kilometres surveyed	Encounter rate (crocodiles/km)
South Road	11	8.3	1.33
Sewage pond	24	1.24	19.35
Grand Belize Estates	13	9.5	1.37
Mahogony Bay	37	16.5	2.24
San Mateo/Grand Caribe	7	8.6	0.81
New South Road	4	5.4	0.74
Croc cove north	4	9.9	0.40
Laguna de San Pedro West	8	12.3	0.65
Laguna de San Pedro South-East	13	15.0	0.87
Laguna de San Pedro North-East	0	4.4	0
South-West coast	6	11.1	0.54
South-East coast	6	13.6	0.44
North-East coast	2	12.9	0.16
North Interior 1	2	2.1	0.95
North Interior 2	4	6.3	0.63
Laguna De Mateo	25	7.7	3.24
North Road	16	4.5	3.56
Bacalar Chico West coast	13	12.4	1.05
Boca channel/Laguna de Cantena	4	11.0	0.36
Totals	199	171.5	1.16*

Nocturnal spotlight surveys

The number of crocodiles encountered was used as a representative sample of the distribution (see Figure 3.3 and Table 3.2) of the discontinuous crocodile population in Ambergris caye. Locations such as the Sewage Pond, North Road, and Laguna De Mateo exhibited remarkably high encounter rates, with 19.35, 3.56, and 3.24 crocodiles per kilometer surveyed, respectively. Grand Belize Estates and Mahogany Bay also show relatively high encounter rates, with 1.37 and 2.24 crocodiles per kilometer surveyed, respectively. On the other hand, locations like Laguna de San Pedro North-East and North-East Coast exhibit encounter rates of 0 and 0.16 crocodiles per kilometer surveyed respectively. A total of 199 American crocodiles were observed over 171.5 km of survey routes (1.16 crocodiles/km) (see details in Table 3.2). Of the 199 crocodiles observed, 59 (30%) were 'eyeshine only' (EO). Hatchlings/yearlings 44 (32%), juveniles 32 (23%), sub-adults 20 (14%), and adults 44 (31%) comprised the remaining 140 crocodiles for which TL could be estimated (see Figure 3.4).

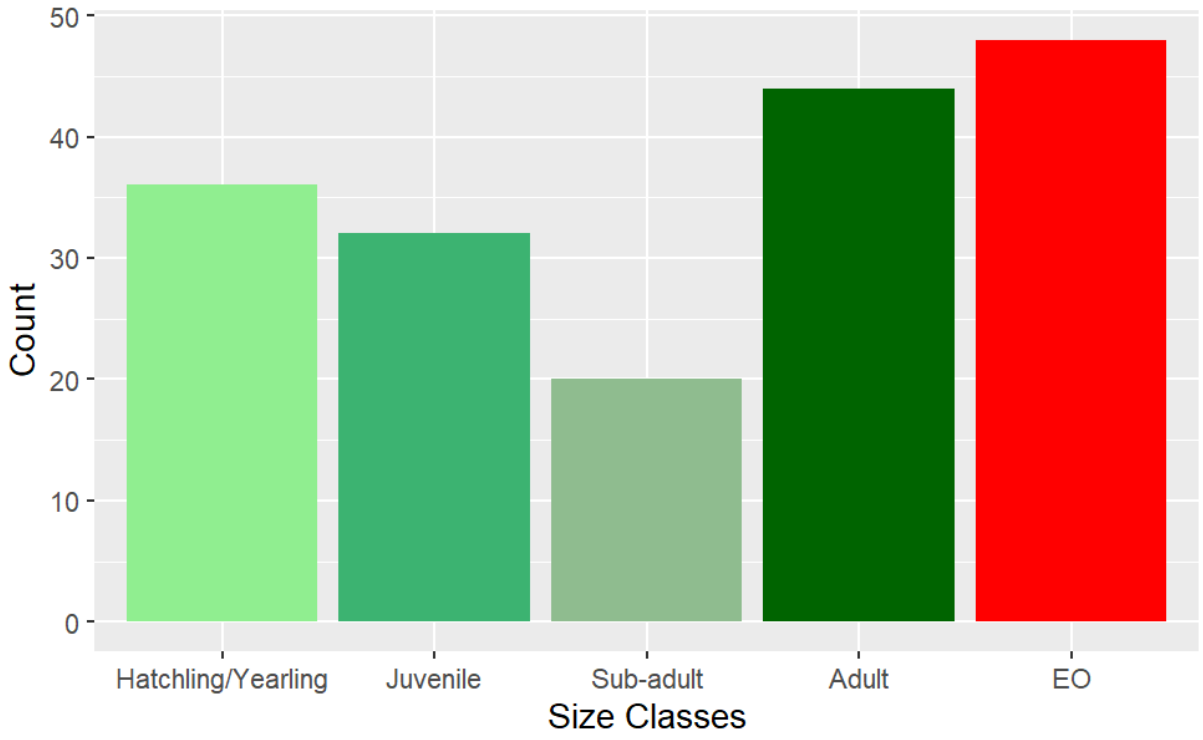

Figure 3.3. Size class distribution of *Crocodylus acutus* observed during nocturnal eyeshine surveys of Ambergris caye, Belize, in 2023. EO refers to eyeshine only, where size could not be determined.

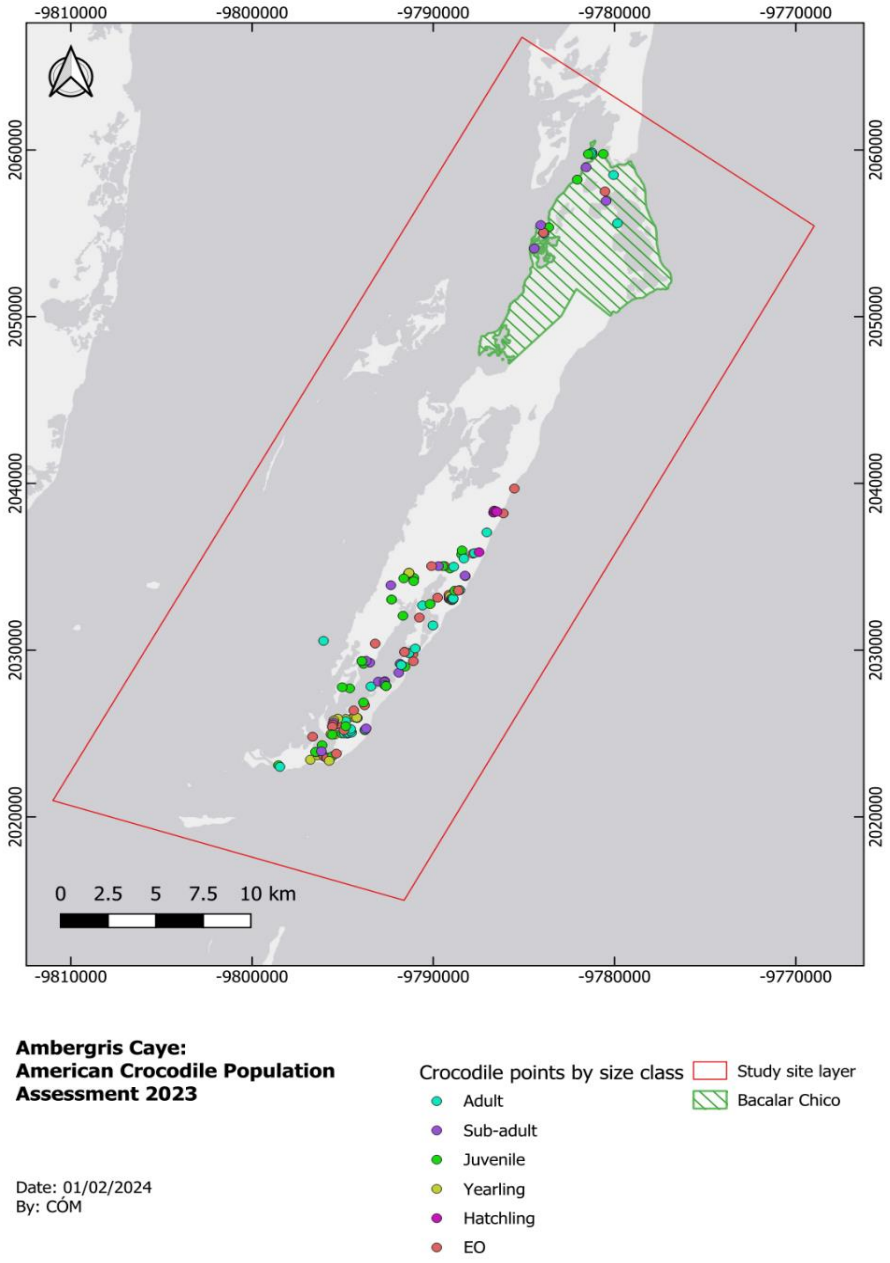

Figure 3.4. Locations of *Crocodylus acutus* observed on nocturnal eyeshine surveys colour coded by size class (see main text) in Ambergris caye. Map generated using QGIS.

Comparing current population to previous population assessment at Ambergris caye

A Wilcoxon rank sum test with continuity correction revealed no significant difference in crocodile encounter rates between the 2023 surveys and those conducted in 2010 - 2011 ($W = 120$; $p = 0.791$; see Table 3.3 and Figure 3.8A).

Table 3.3. Comparison of encounter rates of *Crocodylus acutus* 2010/11 and 2023 in Ambergris caye.

Survey year	Number of crocodiles	Kilometres surveyed	Average encounter rate (crocodiles/km)
2010-11	57	59.56	1.76
2023	182	148.10	2.19

Comparing crocodile encounter rates between habitat types

The Kruskal-Wallis test did not reveal any statistically significant differences between crocodile encounter rates across the different habitats ($W = 4$; $p = 0.406$), with the exception of the sewage pond. The crocodile encounter rate at the sewage pond was significantly higher than all other sites surveyed (19.35 crocodiles /km) (Table 3.4, Figure 3.5 and Figure 3.8C).

Table 3.4. Comparison of average encounter rates of *Crocodylus acutus* surveyed in different habitats of Ambergris caye 2023.

Habitat type	Number of crocodiles	Kilometres surveyed	Average encounter rate (crocodiles/km)	Standard error
Canal	37	16.5	2.24	-
Lagoon	50	50.4	1.02	0.57
Mangrove wetland	61	54.6	1.22	0.35
Ocean	27	50.0	0.55	0.19
Sewage pond	24	1.24	19.35	-

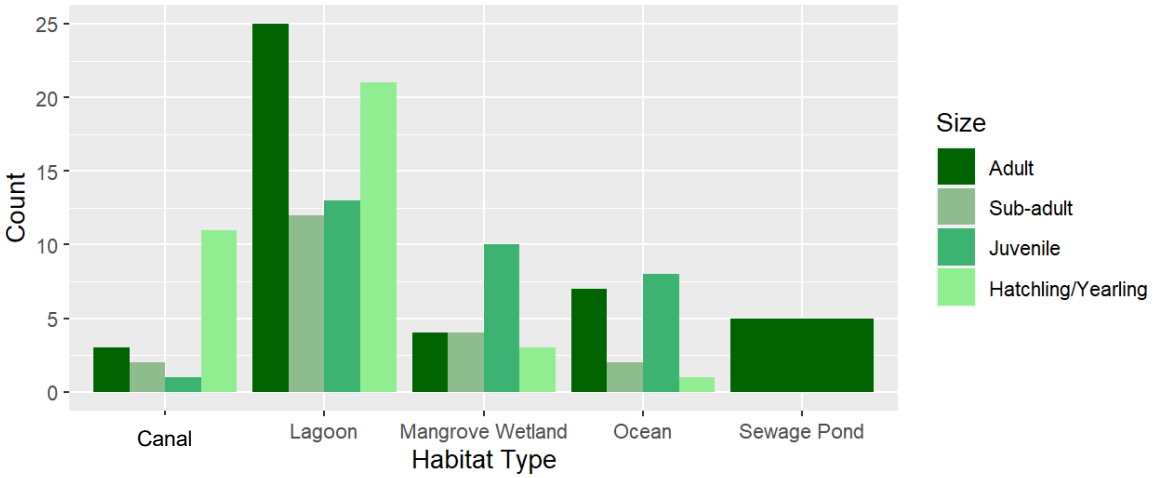

Figure 3.5. Comparison of size estimates of *Crocodylus acutus* in habitats of Ambergris caye.

Two survey areas of particular interest were the sewage treatment pond area and the Coco beach resort area (See Figure 3.6). As previously mentioned, the encounter rate observed at the sewage pond area was exceptionally high. As one of the highest points on the island with loose sandy substrate for nesting and dense surrounding mangrove wetlands with large deep volumes of water in the three sewage ponds, these sites appear to be very attractive to adult crocodiles. Five adults were confirmed to be in the pools, and the status of the other 19 detected crocodiles could not be confirmed. But it appears that only large >200cm adults and smaller hatchlings/yearlings (<60 cm) are present in the pools. A high density of yearlings was observed in the adjacent man-made canal system of the Mahogany Bay resort, while only 2 sub-adults and 1 juvenile were observed in the area.

Figure 3.6. **Top**, map of *Crocodylus acutus* observed during nocturnal eyeshine surveys and nests located at the sewage ponds and surrounding area on Ambergris caye, Belize, 2023. **Bottom**, map of *Crocodylus acutus* observed during nocturnal eyeshine surveys and nests located at the Laguna de Mateo Coco beach resort area on Ambergris

The survey with the highest count of adult crocodiles (9) was the Laguna de Mateo area, with the majority of adults (5) concentrated on the lagoon side of the Coco Beach Resort. The behaviour of crocodiles in this area was notably different than in other locations (Ó'Mórdha, pers obs), with animals at Coco Beach Resort exhibiting less wariness of human presence and in some cases approaching humans.

Comparing crocodile encounter rates between Bacalar Chico and South Ambergris caye

Two surveys were conducted in the BCMRNP area. Seventeen crocodiles were counted over 23.4 km yielding a mean encounter rate of 0.71 crocodiles/km. The structure of the population observed at BCMRNP (juveniles (36%), sub-adults (29%) and adults (36%)) was dissimilar to that of the southern area of Ambergris caye (juveniles (15%), sub-adults (9%) and adults (22%)). Most notably, no individuals <60 cm (hatchlings and yearlings) were observed during surveying of the BCMRNP area (see Figure 3.7).

The Wilcoxon rank-sum test comparing the encounter rates of crocodiles between Bacalar Chico and South Ambergris caye did not reveal a statistically significant difference (W = 13; p-value = 0.655). Therefore, based on the available data, there is no indication that the encounter rates differ significantly between the two locations (Table 3.5 and figure 3.8B).

Table 3.5. Comparison of average encounter rates of *Crocodylus acutus* in the Bacalar Chico National Park and the southern part of Ambergris caye.

Ambergris caye area	Total crocodiles	Total distance covered	Average encounter rate (crocodiles/km)
BCMRNP	17	23.40	0.71
South Ambergris	182	149.34	2.19

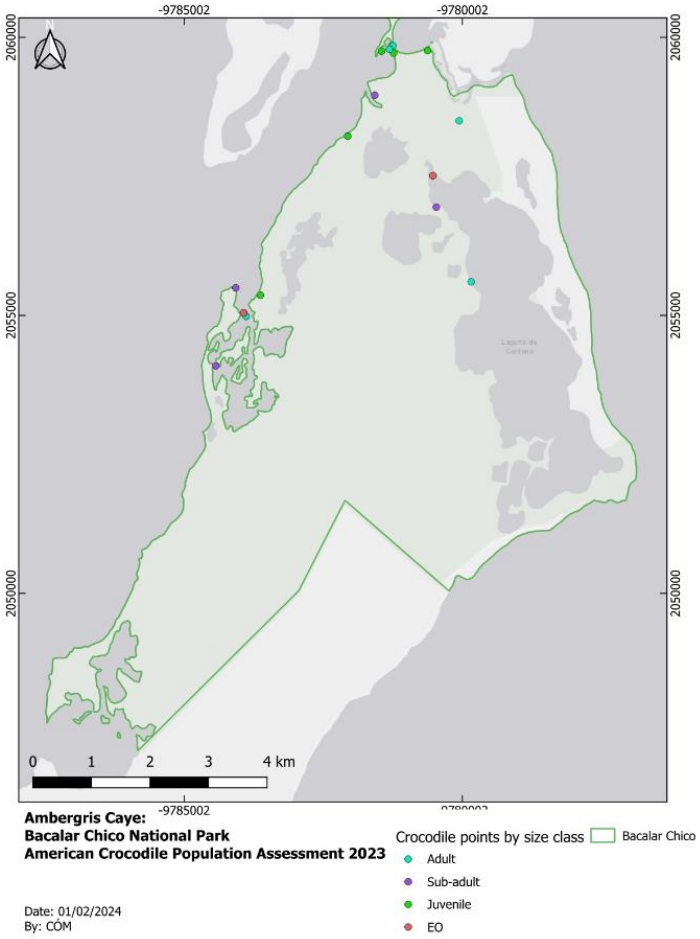

Figure 3.7. Locations of *Crocodylus acutus* observed on nocturnal eyeshine surveys colour coded by size class in the Bacalar Chico National Park in 2023. Map generated using QGIS.

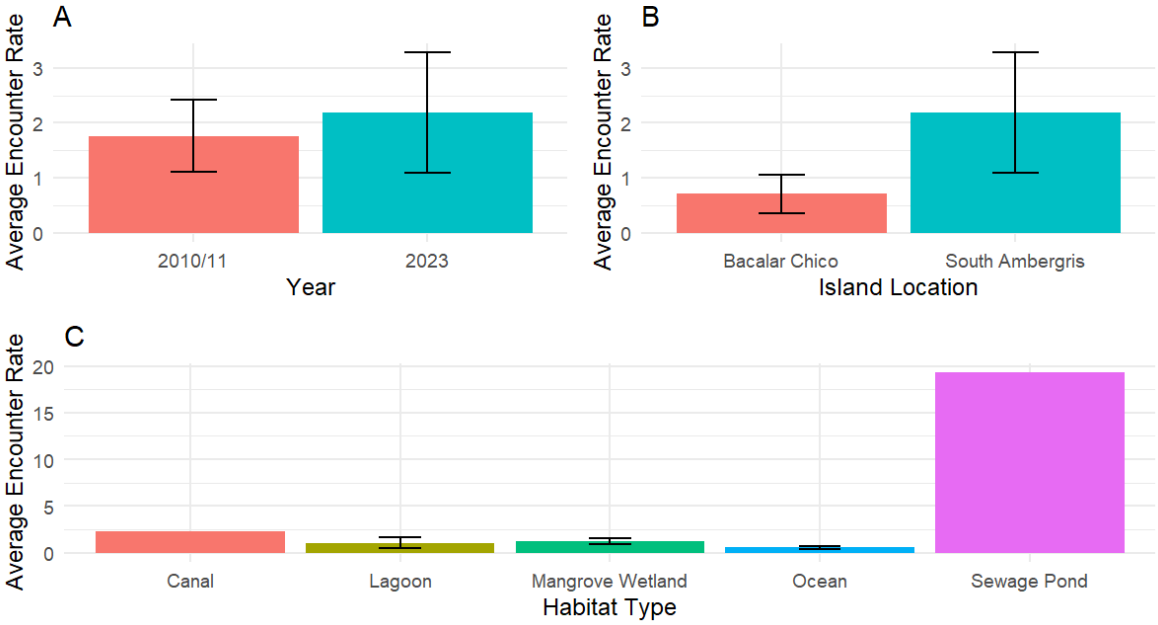

Figure 3.8. A: Average encounter rate of *Crocodylus acutus* surveys for 2010-/11 and 2023. **B:** average encounter rate of *Crocodylus acutus* for Bacalar Chico and south Ambergris caye in 2023. **C:** average encounter rates of *Crocodylus acutus* for habitat types in 2023.

Nesting

The nine nests found during this study ranged between 1.61-8.25 m from the water's edge, excluding one outlier which was found 60.90 m, from the water's edge. Nest elevation ranged between 7-11m, nest width ranged between .50-1.67m, and nest depth ranged between 2.3-5.65m (see Table 3.6). The highest number of nests, five (56%), were located at the local sewage treatment ponds in loose sandy soil (see Figure 3.9). The four other nests were not found in close proximity to any other nests. All nests were found along the eastern outcrop of the caye, which has much more availability of suitable high dry sandy ground then the western shore that is primarily dominated by mangrove wetlands.

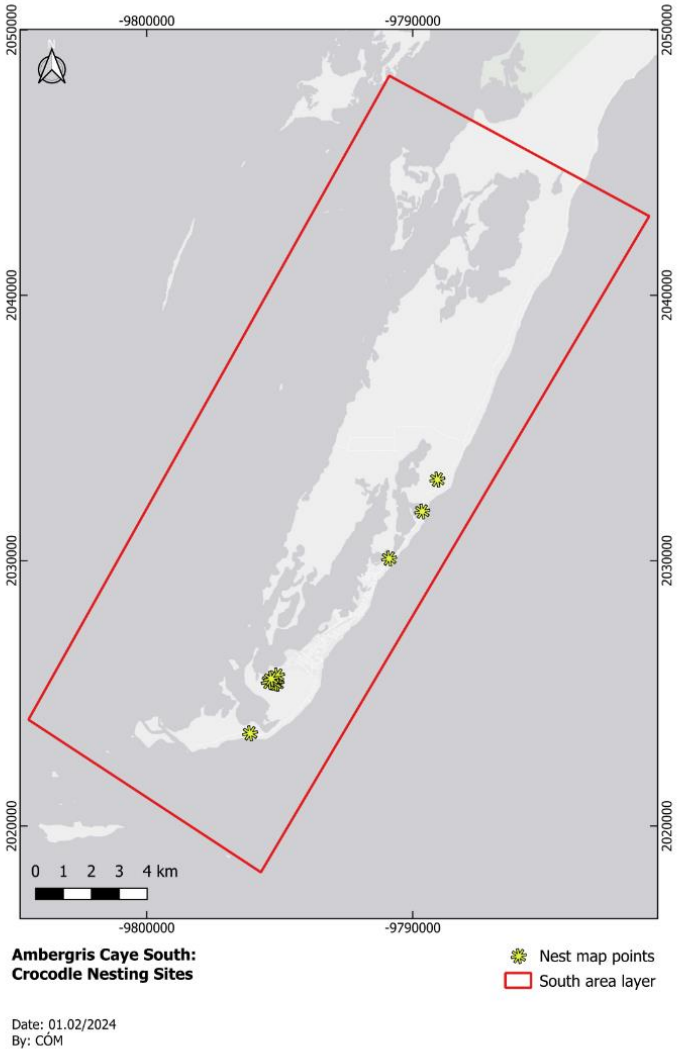

Figure 3.9. Locations of *Crocodylus acutus* nesting sites found in Ambergris caye in 2023. Map generated using QGIS.

Table 3.6. Measurements recorded for all *C. acutus* nests found on Ambergris caye, Belize 2023.

Nest	Distance From Water (m)	Elevation (m)	Nest Width (cm)	Nest Depth (cm)	Substrate
1	5.1	11	-	-	Sand, Pebbles, Concrete, Plastic, Glass
2	6.46	6	87	47	Sand
3	6.88	9	62	56.5	Sand
4	8.25	6	-	45	Sand
5	6.4	11	167	43	Sand
6	1.61	11	112	32	Sand
7	4.24	7	50	23	Sand
8	60.9	7	-	-	Sand
9	-	-	-	-	-

Nest 7 was located after hatching on a small island adjacent to an abandoned hotel construction site. The clutch from Nest 1 was removed with the permission from the Belize Forest Department by ACES Wildlife Rescue on the 19/05/2023, after the NGO was contacted informing them that the nest was located beneath a waste “burn pit” on the property. Eighteen eggs were incubated at the ACES Wildlife Rescue clinic. Fourteen of the eggs hatched successfully on 19 June 2023, and after 7 weeks of observation the hatchlings were released into suitable habitat on 7 August 2023. Nest 8 was found by a local resident who contacted ACES Wildlife Rescue and provided video evidence of a female crocodile digging a hole nest on a private property. Unfortunately, the nest was accidentally destroyed by heavy machinery conducting landscaping activities, resulting in complete clutch failure. The exact location of Nest 9 could not be confirmed as the hatchling “creche”, indicating a nest was nearby, was located at the Coco Beach Resort dumping site. Any evidence of the nest appears to have been disturbed by dumping activities.

Discussion

Population size is a major factor for the survival or extinction of a population. The larger the population the more robust it is against the impacts of abiotic and biotic events as well as stochastic changes to age structure, genetic drift and inbreeding depression (Thompson, 1991; Reed et al., 2003). When trying to determine the minimum viable population (MVP) (the smallest population size required for a species to maintain its viability and survive over the long term, accounting for environmental variability, genetic diversity, and demographic factors).There have been many proposed concepts of quantifying general rules, such as the 50/500 ‘rule of thumb’ (Minimum effective population size of 50 is needed to avoid inbreeding depression in the short term, while 500 individuals are required to maintain genetic diversity and ensure long-term evolutionary potential) (Franklin, 1980; Soule, 1980). Another definition proposed by Shaffer (1981), was the MVP for any given species in any given habitat was ‘the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental and

genetic stochasticity, and natural catastrophe'. More recently Reed et al., (2003) modelled MVP and determined that long-term survival (>40 generations) requires a minimum population size of the order of 5000.

If MVP concepts were applied to American crocodiles in Belize, assuming no overlap with neighbouring populations, they would indicate that the species would likely face extinction unless there was human intervention. Platt and Thorbjarnarnson (2000b) estimated the country wide population of *C. acutus* in Belize to be 358-537. While this is most likely a lower end estimate, even doubling this number would give a total population far below any estimates for a MVP. Considering that the population of crocodiles on Ambergris caye is considered to be insular (Platt and Thorbjarnarson, 2000b; Labarre et al., 2017), whilst the 199 crocodiles counted in our study certainly does not represent the total population of the caye, the 1.2-fold increase in our 2023 encounter rate (1.16 crocodiles/km) compared to that reported in 2020-2011 (0.95 crocodiles/km) (Chenot-Rose, 2013) suggests that the population is stable and may be recovering.

However, it is important to firmly ground what is a necessary population for survival in a complete understanding of crocodilians' unique biology (Webb, Manolis and Whitehead, 1987; Briggs-Gonzalez et al., 2021). High adult survivorship delayed sexual maturity, longevity, and repeated reproductive cycles once adulthood has been reached are key characteristics of the population biology of crocodilians (Kushlan and Mazzotti, 1989). American crocodiles are among the largest organisms in the Belizean ecosystem. Like all crocodilians the increase in size from hatchling to adult are of a magnitude greater than most other vertebrates (Whitaker and Whitaker, 2008). This size discrepancy allows them to occupy different niches at different life stages. Adults are relatively immune from predation, exceptions being from each other and humans (Briggs-Gonzalez et al., 2017).

Furthermore, female crocodilians lay clutches ranging from 10 to 60 eggs (Thorbjarnarson, 1996) and reproduce every 1 to 3 years. Larger females tend to lay larger clutches. It takes approximately 1 decade for females to reach reproductive maturity, and they can live up to 50-70 years. Consequently, a mature female could potentially lay between approximately 133 to 3600 eggs over her lifetime (Thorbjarnarson, 1989).

The robustness and fecundity of adult crocodiles makes them very capable of showing impressive population recovery capacities (Fukuda et al., 2011). While low hatchling survival rates are unlikely to impact a crocodilian population in the short term, a high adult mortality rate can lead to a rapid decline in population (Bishop et al., 2009; Briggs-Gonzalez et al., 2017)

With nine nests observed during the 2023 study period, if every nest was to succeed, between 90-540 hatchlings could hatch each season. If survival rates of the hatchlings are similar to that in other parts of *C. acutus*'s range (Mazzotti et al., 2022; González-Desales et al., 2016), this would have the potential to maintain, if not slowly increase the population over time. The lack of any hatchlings or

yearlings in the areas of the BCMRNP surveyed, may be an indication that no nesting is occurring or that nesting attempts fail, or the habitat is unsuitable for hatchling survival, though more surveying of the area is required to determine the precision of the results found during this study.

All nests found in this study but one were located in suboptimal conditions. Two nests being disturbed, and one being rescued indicates that optimal nesting habitat that is not in close proximity to human activity is extremely limited. *C. acutus* is known across its range to be very inconspicuous and does not nest close to human activity when other options are available (Platt and Thorbjarnarson, 2000a; González-Desales et al., 2016; Mazzotti et al., 2022). Nest 9 being located in the Coco Beach "dumpsite" again shows the lack of suitable available nesting sites.

The dikes adjacent to the sewage ponds by far represent the most concentrated area of nesting known to occur on Ambergris caye. Anecdotally, the sewage ponds have been known as a *C. acutus* nesting site since ACES Wildlife Rescue has been present on the island (2010). The area is relatively undisturbed by human activity. The fact that this area appears to be the only habitat available by *C. acutus* does imply that females have been successfully nesting there historically. On 7 August 2023, 64 hatchlings were counted during a night post-hatching survey near the sewage ponds. The ponds have dense vegetation growing around their perimeters which provides suitable cover hatchlings require for hunting and safety from predation (Somaweera, Brien and Shine, 2013). However, this vegetation is regularly cleared for access to the pools by staff, which may increase the susceptibility of hatchlings to predation. The biochemistry and microbial conditions of the pond water and its potential impacts on the health of hatchlings and mature crocodiles, as well as nest success, is not known; Studies have found negative impacts on reproduction and population decline in *Alligator mississippiensis* attributed to endocrine disrupting chemicals such as organochlorine pesticides, polychlorinated biphenyls (PCBs), and brominated and fluorinated organic pollutants (Guillette et al., 2000). There has been a substantial increase in research on the impact of these compounds over the past three decades, highlighting growing concerns about their effects of environmental contaminants on crocodilian populations, including those in Belize (Wu et al., 2000a, 2000b, 2006; Rainwater et al., 2002, 2007; Pepper et al., 2004; Sherwin et al., 2016)

The other area of significance for *C. acutus* on Ambergris caye is the Coco Beach lagoon side site. It is anecdotally well known as an area that has been regularly used as a crocodile feeding tourism site. Tourists have been documented by ACES Wildlife Rescue being brought to a pier opposite the resort in order to view and directly feed crocodiles. Feeding of crocodiles is well known to induce negative and potentially dangerous changes in behaviour, making them more likely to approach humans, display feeding responses and show less wary behaviour (Chirgwin and Harvey, 1999). Many of the adult crocodiles in the lagoon have been captured and relocated numerous times, particularly from the Coco Beach staff housing site which is built on a flood plain adjacent to the lagoon. These crocodiles

were noted for the unusually high amounts of past scarring and injuries that appear to have occurred via inter-species conflict, again unsurprising given the atypical conditions and behaviours in the area. This is comparable to observations by Rainwater et al. (2011), where an unusually high number of crocodiles congregated beneath a highway bridge along the lower Tarcoles River in Costa Rica. This behaviour was driven by human feeding, resulting in similar conflicts among individuals, particularly large males. These areas likely support dense crocodilian populations primarily due to feeding by humans, which attracts individuals to these locations. Given that American crocodiles are large apex predators, this is particularly worrying as though attacks on humans are relatively unusual, changes in behaviour resulting from both indirect and direct feeding increases the potential for attacks on pets, livestock and humans which can be fatal (Pooley, 2015, 2016; Pooley et al., 2020; Henkanaththegedara et al., 2023; Sideleau et al., 2021, 2022)

Given the extreme close proximity of crocodiles on the island to human habitation, the continuation of these feeding practices whether direct or indirect significantly increase the risk to human life (González-Desales et al., 2021). This is especially true for local residents since many of the most densely human-populated areas of the islands, which are local estates that regularly flood, are on the lagoon side of the island and built on stilts above lagoons. Crocodiles were regularly observed underneath these residences during this field study and on multiple occasions crocodiles were removed. The localised densities of adult crocodiles in the Coco Beach area appear to impact the occurrence of intraspecies conflict, with many of the animals removed from residences having scars, injuries and wounds most likely from intraspecies conflict. American crocodiles are not known to be a particularly social species and mature individuals do not tend to occur in such localised densities with the exception for breeding and nesting (Thorbjarnarson, 1989; Rainwater et al., 2011).

The highest density of yearlings, 56% of all yearlings surveyed, was found in the canals and wetlands surrounding the sewage ponds, indicating that this is the most successful nesting area on the island. Further research is needed to assess the survival rates of hatchlings in this key nesting site, and policies need to be implemented to ensure that any activities being carried out on the site take into account the importance of the site for crocodile nesting and be performed in a way that does not negatively impact the crocodile nesting success.

In the present survey, mature adults comprised a large portion (31%) of crocodiles whose size could be estimated. Juveniles (23%) and sub-adults (14%) made up a smaller proportion. Fifty-five percent (55%) of all crocodiles whose size was estimated were juveniles, yearlings and hatchlings. This high proportion of young crocodiles is consistent with signs of a recovering population, similar to that observed previously in 2010-2011 in Ambergris caye (Chenot-Rose, 2013), Caye Caulker (Belize) (Tellez, Boucher and Kohlman, 2016) and in Costa Rica (Mauger et al., 2012). The relatively high percentage of adults and low proportion of juveniles and sub-adults in the present study compared to

that of American crocodiles in regions with higher encounter rates (e.g Costa Rica; Mauger et al., 2012) indicates limited recruitment. Low recruitment may be caused by reproductive failures (i.e. low hatchling success and/or infertility), high levels of predation among neonates and young juveniles, or a lack of nesting due to limited suitable nesting sites (Chenot-Rose, 2013).

Because of the variability inherent in spotlight counts, long-term monitoring is generally required to detect population changes (Bayliss, 1987). The encounter rate in Ambergris caye during 2023 was somewhat greater (1.2-fold) than previously reported (0.95 crocodiles/km; Chenot-Rose, 2013), although not significantly different. This appears to show that the Ambergris caye crocodile population has not significantly increased over the past 20 years. This is concerning, as while the encounter rate on Ambergris caye is one of the highest recorded in Belize, is much lower when compared to *C. acutus* encounter rates across the animal's geographic range (Mauger et al., 2012).

While the American crocodile population in Ambergris caye appears to have remained relatively stable, the pressures facing *C. acutus* such as habitat loss, particularly that of nest sites, are only likely to increase in the following decades (Sweetman et al., 2019). The recruitment rate of hatchlings is not known, but the overall population is highly unlikely to increase (and more likely to decrease) in the following decades if the rapid poorly managed development of the island's limited remaining wetlands and sand banks continues along its current trend. The crocodile population may be near the island's current carrying capacity, and due to limited nest sites and increased human-crocodile interactions, it is unlikely to improve without a species management strategy.

The first population surveys of the BCMRNP were carried out in this study with no historic records with which to compare. Unfortunately, due to time and resource constraints the survey area was limited to the western shore, the Boca channel, and the Northern half of the Laguna de Cantena. While the encounter rate was not significantly lower compared to the southern part of Ambergris caye, no yearlings or hatchlings were observed in the area. Nesting activity was also not observed. nor any suitable nesting beaches found in the areas surveyed, suggesting crocodiles found in the area are potentially transient or displaced. Such individuals may be coming from the southern area of the island or from the north in the Mexican region of the Yucatan, both possibly due to conspecific competition. Surveying of the eastern shore of BCMRNP is essential to determine what nesting activity, if any, is occuring there. Worryingly, in 2007 a substantial area of beachfront along the eastern shore of the BCMRNP was sold, is now owned privately, and is currently for sale for the development of both private residences and resorts. The remaining unsold beachfront may be suitable for crocodile nesting and must be further investigated, especially given that much of this property has been sold and de-reserved.

Concluding comments

The resilience of crocodile populations to overexploitation becomes evident through the positive responses observed with the implementation of protective measures (Bayliss, 1987b). Specifically, American crocodile populations have demonstrated swift recovery subsequent to the prohibition of commercial hunting activities (Ross, 1998). In a comprehensive study assessing the nationwide status of American crocodiles in Belize, Platt and Thorbjarnarnson (2000b) pinpointed Turneffe atoll as a key player in regional population dynamics. Subsequent investigations by Rainwater and Platt (2009) revisited Turneffe atoll, revealing a notable decline in both nesting activity and population size. The overall encounter rates in 2008 were 2.7-, 3.5-, and 3.6-fold lower than those observed in 1996, 1997, and 2002. This decline, particularly in the number of nests discovered (2 in 2008), marked a substantial departure from previous years, which had peaked at 16 in 2004. While this initial reduction in nesting activity coincided with human alterations to recognized nesting beaches on the atoll, subsequent surveys conducted between 2009 and 2012 indicated that encounter rates and nesting effort had rebounded and exceeded those observed in 1996, 1997, and 2002 (Platt and Rainwater., 2014). This recovery suggests that the earlier decline was more likely attributable to seasonal variability rather than permanent population declines, emphasizing the critical importance of long-term population monitoring. Considering all population studies conducted previously in Belize (refer to Table 3.1), a consensus emerges regarding the importance of management and conservation efforts, with a particular emphasis on safeguarding critical nesting beaches. The findings underscore the intricate relationship between human activities and the well-being of crocodile populations, highlighting the need for strategic conservation initiatives to preserve their habitats and ensure the continued success of protective measures.

Previous countrywide surveys did not consider hybridisation between *C. morletti* and *C. acutus* due to limited understanding at the time (Platt and Thorbjarnarnson, 2000b). However, hybridisation is now recognised as significant along coastal mainland zones (Hekkala et al., 2015; Wilkie et al., 2024), emphasising the importance of studying island populations of *C. acutus* where such hybridisation appears absent. This investigation aims to spotlight Ambergris caye as a crucial area for *C. acutus* in Belize, likely contributing to the regional metapopulation dynamics of American crocodiles. Further research is recommended to confirm the presence/absence of hybridization within the Ambergris caye population.

The American crocodile population on Ambergris caye exhibits a remarkable resilience to intense anthropogenic pressures (Sweetman et al., 2019; Palafox et al., 2022). The discovery of nine nests, likely not an exhaustive count for the island, as surveying the entire caye for nest sites was outside the

scope of this study, is particularly noteworthy considering most of the beaches on the caye are highly developed. In the absence of elevated beach ridges—now largely absent due to development outside the BCRMNP area—the sewage pond area emerges as a crucial site for continued reproductive success of *C. acutus* on Ambergris caye. However, the low levels of hatchling and juvenile crocodiles suggest suboptimal conditions for survival to adulthood.

The absence of nesting in the BCRMNP does not necessarily indicate a lack of nesting activity. The surveyed area was limited and did not encompass all habitats conducive to nesting. Of concern are the eastern beach ridges, once part of the park and potentially serving as ideal crocodile nesting habitat but now occupied by private residences or resorts. A strong recommendation is made for further surveys to explore potential nesting sites throughout the BCMRNP area, with a particular emphasis on the remaining beach ridges along the eastern shore still within the park's boundaries. Ensuring the future protection of remaining land within the BCRMNP is crucial to maintaining the ecological integrity of the region.

Acknowledging the limitations of this study is essential. Surveys were conducted exclusively during the period from May to September 2023, which precluded the assessment of seasonal variability and limits the ability to detect annual fluctuations in crocodile numbers and nesting effort. Surveys over multiple, preferably consecutive, years are critical for identifying these variations, as demonstrated by long-term monitoring efforts at Turneffe atoll. For example, Rainwater and Platt (2009) initially reported a notable decline in the crocodile population and nesting activity at Turneffe. However, subsequent surveys conducted from 2009 to 2012 revealed that the population and nesting effort had returned to or exceeded earlier levels, emphasizing the importance long term monitoring to account for annual variability.

Additionally, the inability to survey all areas within and around Ambergris caye further limits the robustness of encounter rate and nesting effort estimates. Time and funding constraints were significant contributing factors to these limitations. This study provides an essential baseline for continued monitoring efforts, and future research should aim to address these constraints to develop a more comprehensive understanding of the cayes crocodile population.

Additionally, implementing more direct methods for population recovery could prove beneficial given the developed nature of the island and local infrastructure. Crocodilian management programs generally fall into two main categories: standard conservation protection measures (e.g., legislation, prohibited killing, protected areas, reintroductions) and active management programs based on sustainable use. Despite the implementation of standard conservation practices in Belize since 1981, there has been limited recovery, suggesting a potential failure to address critical issues hindering population recovery, such as habitat/nesting site loss and opportunistic hunting.

A significant challenge to effective conservation in Belize is enforcement. While legislation prohibiting killing and the establishment of protected areas exist on paper, they are not consistently enforced. Other pressing issues include the accidental drowning of crocodiles in fishing nets and the continued approval of development in critical habitats, which further undermine the efficacy of conservation efforts (Platt and Rainwater., 2014).

According to the Crocodile Specialist Group (CSG), there are three primary ways in which crocodiles can be exploited for both commercial gain and conservation benefit: direct harvest from the wild, ranching, and captive breeding ("farming" or "closed cycle captive breeding"). Each method comes with its own set of advantages and disadvantages (David, 1994), and the appropriateness of each is highly dependent on various factors, including the regional context, species involved, and economic considerations.

While we do not suggest these strategies are currently suitable for American crocodiles in Belize, due to the lack of enforcement against opportunistic hunting and the absence of a permanent presence of Belize Forest Department officers on Ambergris caye, coupled with the lack of long term population monitoring. Addressing these issues could potentially make them viable methods for future successful enhancement of recovery. Specifically, we recommend exploring a head-starting program, a management strategy involving rearing wild-caught hatchlings in captivity until reaching a body size less vulnerable to predation, followed by release into suitable habitat (Van de Ven et al., 2009; Van Weerd et al., 2008; Antelo et al., 2010; Muñoz et al., 2000). Furthermore, establishing a long-term population monitoring program based on nest counts and nocturnal spotlight surveys is crucial for accurately determining population trends and assessing the effectiveness of any conservation strategies.

A key recommendation emerging from this study advocates for the establishment of a responsible tourism industry coupled with an education program (Ploeg et al., 2011; Lemos, 2017). This initiative should focus on creating local awareness and underscoring the ecological significance of the American crocodile as a flagship species for the island's ecosystem and wetlands.

To ensure the survival of the species, a comprehensive management and recovery plan detailing short-term and long-term goals needs to be devised. The implementation of such a plan should be done in collaboration with and receive approval from the Belize Forest Department. This plan should integrate construction practices featuring barriers aligned with the behavioural patterns and needs of the crocodile population residing in close proximity to human habitats. Additionally, it should prioritise enhancing the safety of human residents coexisting with crocodiles.

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Chapter 4

Morphometrics and growth rates of American crocodiles in Ambergris caye, Belize

Abstract

Recent evidence suggests that the cayes and atolls of Belize are the primary strongholds of the American crocodile *(Crocodylus acutus)* in Belize. This study utilised 13 years of crocodile capture data (n=865 crocodiles) in the Ambergris caye population to determine growth rates, morphometrics, sex ratio and sexual size dimorphism. Animals exceeding a TL of 60cm were scanned for a radio frequency identification microchip (RFID) to ascertain any prior capture records Total length (TL) growth rates, based on 115 recaptured crocodiles, were calculated as 0.045 ± 0.027 cm/day.

Females (n = 20) were found to have a slightly lower growth rate than males (n = 47), with females exhibiting an average growth rate of 0.039 ± 0.028 cm/day compared to 0.048 ± 0.028 cm/day in males. However, these differences were not found to be statistically significant. . A stronger negative relationship between growth rate and total length (TL) was observed in females, with growth rate decreasing more significantly as TL increased compared to males. Males TL did not show a significant relationship to growth rate. Growth rates for the Ambergris caye population are relatively low compared with those found in other parts of *C. acutus*'s range. The sample used for morphometric analysis included 565 juveniles (TL<120cm), 93 sub-adults (120≤ TL<180 cm) and 207 adults (TL>180 cm). Both positive and negative allometric relationships were found between body length metrics (TL) and other morphometrics. All morphometric regressions were linear. The dorsal cranial length:cranial width (DCL:CW) ratio of 2.7 to 4.2 was calculated, a broad-snouted skull morphotype similar to that found in other island populations of *C. acutus* in the Yucatan region. The sexual dimorphism index of 1.07 towards males suggests a much smaller difference between the TL of males and females on Ambergris caye. Sexual dimorphism of *C. acutus* in the region appears to be less pronounced than in other crocodilians. The functional sex ratio 2.39(M):1.0(F) was very biased towards males, implying that male behavioural characteristics may contribute to their higher likelihood of requiring removal from human-inhabited areas, hence more needing to be captured, or that there exists a selective pressure leading to a bias towards males, or a combination of both factors.

Introduction

Knowledge of individual body size and sex is necessary for analysis of animal population ecology and structure. Basic morphometric data (e.g. total length, cranial shape, mass) can help researchers answer complex questions about sexual size dimorphism (Roth and Mercer, 2000), hybridisation (Strauss, 2012), prey selection (Iijima, 2017), energetic constraints (Campbell et al., 2010) and different ecological niches (Staniewicz et al., 2018).

In the conservation management of crocodilians, in particular, this knowledge is indispensable. The assessment of individual body size and population size-class structure holds paramount importance as size, rather than age, serves as the primary determinant of demographic and reproductive processes (Thorbjarnarson, 1989; 1996; Kofron, 1990). Thus, accurate morphometric data are critical for the development of effective conservation strategies and the preservation of crocodilian populations.

Variability in growth rate, size-at-age, and other life history parameters within populations and among species (Pianka, 1970) and populations (Lindgren and Laurila, 2005) has long been recognized in ecological studies (Parma and Deriso, 1990; Hutchings, 1993; 1997; Gurney and Veitch, 2007; Vincenzi et al., 2014). This individual variation holds crucial significance in evolutionary ecology, having been extensively quantified and studied in various systems (Nussey, Wilson and Brommer, 2007; Clutton-Brock and Sheldon, 2010; Wilson and Nussey, 2010; Dall et al., 2012).

A central focus for ecologists lies in understanding how the diverse growth and life-history strategies exhibited by individuals translate into variations in lifetime reproductive success (Mann et al., 2000.; Krüger and Lindström, 2001; Altmann and Alberts, 2003). The ramifications of such individual variation, particularly in long-lived species, unfold over extended periods of time, necessitating comprehensive, long-term investigations. Historically, studies exploring the fitness consequences of life-history variation have predominantly centred on avian and mammalian taxa (Rollinson and Rowe, 2015). This bias likely stems from the relatively straightforward quantification of fecundity and survival in these taxa compared to ectotherms, which often possess more cryptic reproductive behaviours and higher fecundity rates, posing challenges in linking offspring to specific females. However, overlooking ectothermic species in these studies presents a significant gap, given their unique traits not observed in avian and mammalian groups.

Despite the widespread geographic distribution of *C. acutus*, relatively few studies have investigated the growth rates of this species in the wild. Data are available for some populations in Florida (Mazzotti et al., 2009), along the Caribbean and Pacific coasts of Mexico (García-Grajales et al., Buenrostro-Silva and Charruau, 2012),and the Yucatan Peninsula (Labarre et al., 2017). Although some additional studies provide insights into growth rates for both captive and wild crocodiles, many

are constrained by limited sample sizes (García-Grajales, Buenrostro Silva and Charruau, 2012; Briggs-Gonzalez et al., 2017).

Furthermore, the determination of size at sexual maturity in American crocodiles remains contentious and unclear. Regarding the minimum reproductive size of females, a wide spectrum of data exist, ranging from 180 cm to 280 cm total length (TL) (Platt and Thorbjarnarson, 2000b; 2000a; Charruau, Throbjarnarnson and Hénaut, 2010). For males, reports indicate a minimum size at sexual maturity of 199 cm. More recent studies place minimum reproductive size for females and males at 180 cm (Balaguera-Reina et al., 2015; Labarre et al., 2017). The maximum TL of the species can reach notable dimensions, with large males exceeding 600 cm (Thorbjarnarson, 2010) and over 900 kg in mass (Rainwater et al. 2010), and records documenting females surpassing 400 cm TL (Domínquez-Laso, 2009). These maximum sizes and the age at sexual maturity are likely influenced by resource availability and habitat quality. Understanding these factors is crucial, as they directly impact the functional sex ratio, which considers the proportion of reproductively active males and females in a population. While the sex ratio provides a demographic snapshot, the functional sex ratio reflects the reproductive potential of the population, emphasizing the importance of monitoring sexually mature individuals when assessing population health and sustainability.

The present investigation had the following objectives:

(1) To analyse American crocodile morphometric data collected by the ACES Wildlife Rescue NGO on Ambergris caye, Belize.

(2) To analyse growth rates of *C. acutus* in Ambergris caye.

By pursuing these objectives, this research endeavours to contribute valuable insights into the dynamics of American crocodile populations, particularly in the context of morphology, growth rates and conservation strategies tailored to the unique ecological setting of Ambergris caye.

Materials and methods

ACES Wildlife Rescue has been a wildlife conservation, rehabilitation and research NGO non-profit organisation based on Ambergris caye since 2010. Previously known by its acronym ACES (American Crocodile Education Sanctuary), it was changed to its present name in 2021. As Ambergris caye does not have Belize Forest Department Officers permanently based on the island, ACES Wildlife Rescue is the first and only group competently trained and approved to respond to human-crocodile conflict on the caye. Between 2011–2023, ACES Wildlife Rescue collected morphometric data on crocodiles that they captured (I assisted in 2023). The majority of crocodile captures occur in response to situations where relocation becomes imperative, due to hazards posed to either human safety, crocodile welfare, or both. Additionally, a series of spotlight and nest surveys, led by Chenot-Rose (2013), were conducted in 2010-11 during which captures were carried as part of population

assessments and both morphometric and health-related data were collected. The data collected in 2010-11 used the same methodology as that used through 2023, hence the former were pooled with the latter and collectively utilised in the current analysis of the American crocodile morphometrics and growth rates on Ambergris caye.

Figure. 4.1. Top jaw noose with tension applied allowing researcher to manoeuvre an adult American crocodile, Ambergris caye, Belize. Source: Ciarán Ó Mórdha.

Capture methods varied based on the specific circumstances, environmental conditions, risk factors, animal size, and animal health status (Ciarán Ó Mórdha, pers. obs). For crocodiles measuring less than 120 cm in total length (TL), hand capture has proven to be an effective approach. This method involves grasping the animal behind the head at the neck and restraining it using both hands. For sub-adults 121-179 cm TL, based on minimum reproductive size for females and males at 180 cm (Balaguera-Reina et al., 2015; Labarre et al., 2017) and adults (≥180 cm), the preferred technique is noosing. This method entails utilizing a 2-meter PVC pole with a rope affixed to it (see Figure. 4.1). A "top jaw" self-locking noose is tied to the end of the rope, tightening upon pulling. The noose is secured to the pole with insulating tape, wrapped with a single revolution around the pole's end. The pole is then manoeuvred to guide the noose toward the crocodile's head, slipping it over the top jaw. Once the noose passes halfway into the mouth, the pole is pushed forward while simultaneously pulling the rope backward, tearing the insulating tape. This action allows the pole to be removed, while the noose tightens around the top jaw of the crocodile. Subsequently, the animal can be pulled onto a boat or shore. To further secure the animal, another noose, known as a safety rope, is run down

the top jaw rope, wrapping over both the bottom and top jaws. When pulled, this noose closes the animal's mouth, effectively securing it, as long as tension is maintained on the rope.
In situations where close proximity to the animal is not feasible, two alternative techniques are commonly employed, these are culvert traps and snares.

Figure. 4.2. Culvert trap used to bait and trap nuisance crocodiles by ACES Wildlife Rescue. Source: Ciarán Ó Mórdha.

The culvert trap construction (see. Figure. 4.2) involves utilizing a culvert pipe, sized appropriately for the target animal. A wooden frame is crafted and affixed to the front entrance, while the rear is enclosed with a sturdy material to prevent the animal's escape. A U-shaped metal guide is installed along the vertical sides of the door frame, facilitating the sliding motion of the front door. The door remains suspended by a tripping metal mechanism, connected to a rope tied around the bait (typically chicken) and routed through a hole drilled at the culvert's end. The trap is then set up in a suitable area that will not flood or be swept away by tides. When the crocodile engages with the bait, triggering the tripping mechanism, the door is released, sliding shut and securely containing the animal.
Subsequently, the crocodile can be safely transported within the trap or subjected to restraint using the top jaw method.

A snare is fashioned by creating a circular arrangement of foliage along the water's edge, using young, flexible saplings and surrounding vegetation. Within this circle, a noose made of rope is positioned and concealed. Bait, typically chicken, is strategically placed on the opposite side of the noose to entice the animal through. Alternatively, the bait may be attached to a rope and thrown to the animal to lure it into the noose immediately, although this tactic may prove ineffective if the animal is cautious and should not be used on animals not previously fed by humans. The trapper, holding the rope with the noose, remains motionless and quiet, out of sight until the animal approaches the bait. As soon as the animal's forelimbs pass through the noose, the trapper swiftly moves away from the animal, utilising tension to tighten the noose around the animal beneath its forelimbs. This action effectively captures the animal, allowing for further restraint using the top jaw method by the capturer.

For each animal, ACES Wildlife Rescue aimed to record the following measurements (see Figure 4.3 & 4.4), although, due to the variable nature of captures and risks, not all measurements could be collected for every animal:

1. Total length (TL): distance from the tip of the snout to the tip of the tail, measured dorsally.
2. Snout-vent length posterior (SVLp): distance from the tip of the snout to the posterior margin of the cloacal vent, measured ventrally.
3. Snout-vent length anterior (SVLa): distance from the tip of the snout to the anterior margin of the cloacal vent, measured ventrally.
4. Cranial width (CW): maximum distance between the surangular bones at the level of jaw articulation.
5. Dorsal cranial length (DCL): maximum distance between the tip of the snout to the posterior edge of the supraoccipital bone.
6. Snout length (SL): maximum distance between the tip of the snout to the anterior border of the orbits.

TL, SVLp, SVLa and DCL, are used as body length indicators in many crocodilian studies (Amanya, 2023), whereas measurements such as tail girth, mid-body girth and neck girth are volumetric indicators of body condition (Zweig et al., 2004). The body measurements collected during this study are consistent with those taken in other crocodilian morphometric studies (Webb and Messel, 1978; Hutton, 1987; Platt et al., 2009, 2011; Warner et al., 2016). All body measurements were collected using a fiberglass measuring tape or plastic sewing tape (±1 mm).

Determination of a crocodile's sex is performed by manually probing the cloacal vent for the presence of a penis (cloacal examination of the genitalia). (Brazaitis, 1968). This is typically only done with sub-adults and adults (≥120cm), since in juveniles (< 120cm long) it is not possible to safely probe the cloaca, and the genitalia in hatchlings are generally not developed enough to determine yet whether the individual is male or female. A speculum can be used but for this study it was not (Allsteadt and Lang., 1995).

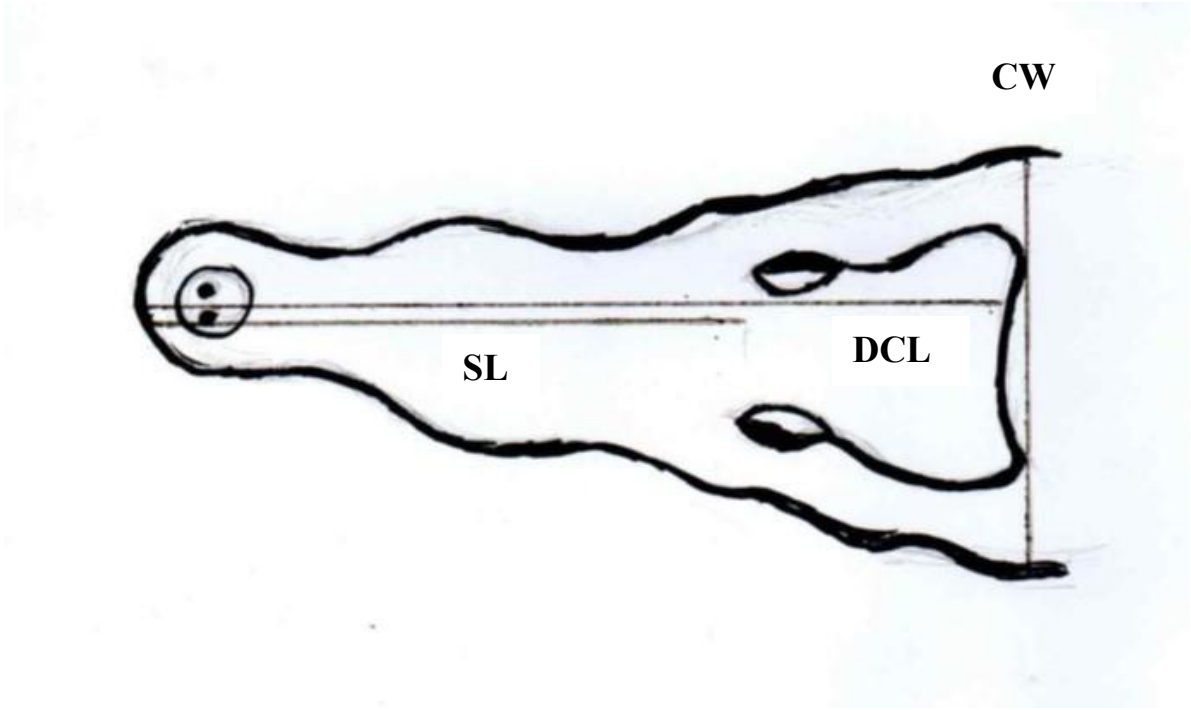

Figure 4.3. Dorsal view of an American crocodile (*Crocodylus acutus*) head showing measurements of dorsal cranial length (DCL), snout length (SL) and cranial width (CW).

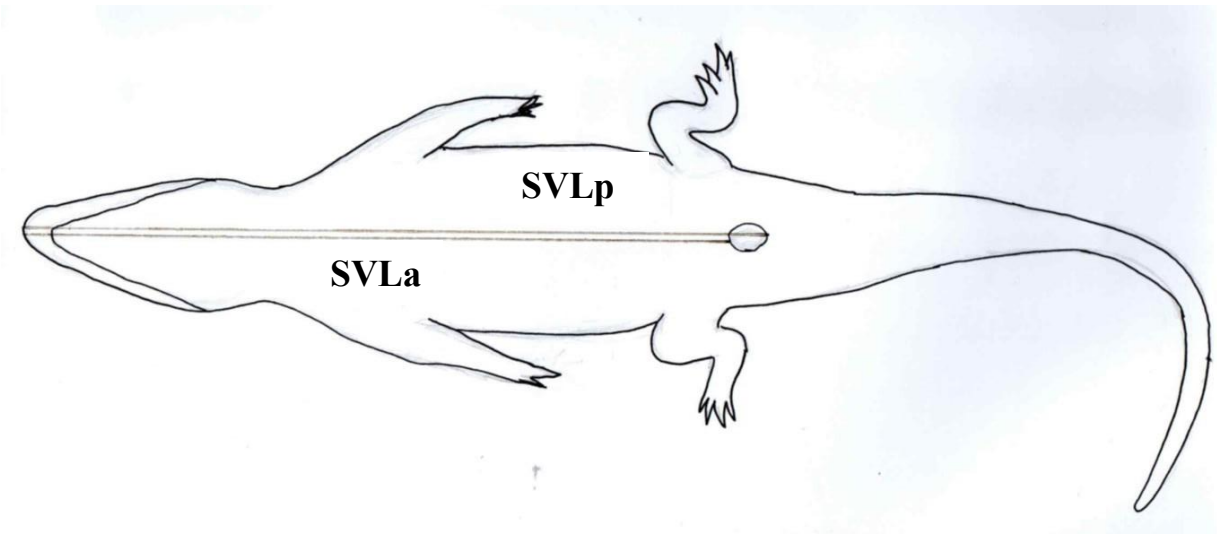

Figure 4.4. Ventral view of an American crocodile (*Crocodylus acutus*) body showing measurements of snout vent length anterior (SVLa) and snout vent length posterior (SVLp).

In the analysis of the morphometric data, American crocodiles were classified by size class following Platt and Thorbjarnarson (2000b). Hatchlings (TL < 30 cm), yearlings (TL = 30-60 cm), juveniles (TL = 61-120 cm), sub-adults (TL = 121-180 cm) and adults (TL>180 cm). For analysis of growth rates and morphometrics all crocodiles whose TL was <120 cm were grouped as juveniles and sex was not considered.

Animals exceeding a TL of 60 cm were scanned for a radio frequency identification microchip (RFID) to ascertain if an individual had been previously captured. Animals smaller than this were not outfitted with an RFID chip due to their small size and lower survival probability. If an animal was not previously tagged, a sterile RFID chip (USDA 840 ID mini microchip) was injected into its tail. Chip injection involved the insertion of the chip via a 15-gauge needle into the tail, positioned at the mid-lateral left-hand side, four scutes behind the cloaca (see Figure. 4.5). Each RFID tag beared a distinct 15-digit barcode that served to identify the individual animal. Upon injection, a scanner (see Figure. 4.6) verified the chip's presence, and the associated barcode was logged, thereby identifying the animal.

For crocodiles measuring less than 60 cm in total length (TL), the scute clipping method was employed for secondary identification purposes. This process involves counting the posterior scutes of the tail, starting from the base and moving upwards in the hundreds. As the scutes diverge dorsally into two rows, the left-hand side scutes are numbered in multiples of ten (e.g., 10, 20, 30), while the right-hand side scutes are counted as singles (e.g., 1, 2, 3). This numbering system allows for the dentification of individual crocodiles based on the scutes clipped, with numbers potentially reaching up to three digits.

Fig 4.5. Injection of RFID microchip at the mid-lateral left-hand side, four scutes behind the cloaca of a juvenile American crocodile. Source: ACES Wildlife Rescue.

Fig. 4.6. RFID microchip scanner displaying sixteen-digit ID code for a juvenile American crocodile. Source: Ciarán Ó Mórdha.

Data analysis

The sex ratio (defined as the relative proportion of sexually mature males to sexually mature females (Platt et al., 2011; Warner et al., 2016)) was calculated and was compared to a 1:1 expected Fisherian frequency using a Pearson's chi-squared test (Using Yates correction for continuity) (Platt et al., 2011; Warner et al., 2016).

Animals were categorised into the following groups: male adults, female adults, male subadults, female sub-adults and juveniles. The analysis of morphometrics exclusively utilized data from the initial capture, excluding any subsequent recaptures from consideration.

In this study, a compressed Sexual Size Dimorphism Index (SDI) was computed to assess the extent of sexual size dimorphism between adult males and females (Lovich and Gibbons, 1992; Platt et al., 2009, 2011; Warner et al., 2016; Labarre et al., 2017). The SDI is a unitless measure obtained by dividing the mean size of the larger sex by the mean size of the smaller sex. If males are the larger sex, one is added to this ratio; conversely, if females are larger, one is subtracted (Lovich and Gibbons, 1992). While SDI can theoretically be based on any measurement or mass, SVLp (Snout Vent Length posterior) was chosen. SVL is widely used in herpetological research and consistency with prior crocodilian studies (Platt et al., 2009; Labarre et al., 2017).

Correlations between each of the morphological measures (TL, SL, DCL, SVLa, SVLp) were investigated by linear regressions between the 5 crocodile groups (male adults, female adults, male subadults, female sub-adults and juveniles). All morphometrics were log transformed to help meet statistical assumptions, enhance interpretability, and improve the robustness of analyses. The ratio DCL:CW was calculated, and the relationship between CW, DCL, and SVLp was investigated using a linear regression.

Growth rates were calculated using data from animals captured more than once during the study period, by dividing growth in length (TL recapture – TL initial capture) by the number of days between captures. A Linear regression was performed between TL Growth Rate (cm/d) and mean TL of individuals between their initial capture and recapture (mm). The data was subsetted by sex and a linear regression was performed same as above to both male and female subsets. A Welch sample t-test was used to compare male vs female growth rates. Tukey's Honestly Significant Difference (HSD) test was used to compare the adult, subadult and juvenile size class growth rates. All statistical analysis was carried out using Rstudio version 4.3.2. The normality of the data was tested , using Anderson darling tests, separately for adult males, adult females, subadult males, subadult females and juveniles.

Results

Population structure and sex ratio

ACES recorded 865 crocodile capture events between 2011-2023. Six hundred thirteen (613) individual crocodiles were captured over the 13 years, 219 were recaptured once, 50 recaptured twice, 17 recaptured three times, 7 four times and 3 five times. Of the 819 crocodiles whose TL was recorded, almost a quarter (23.9%, n= 207) were mature adults, 10.8% (n= 93) were subadults, while the remaining 65.3% (n= 565) of the sample were juveniles (Figure. 4.7). Adults were comprised of 70% males and 30% females, and sub-adults were comprised of 53.8% males and 46.2% females. As mentioned, above sex could not be determined in juveniles.

Based on the combined data for adults and subadults, the sex ratio of males to females in the Ambergris caye population was 1.88(M):1.0(F); However, the functional sex ratio was 2.39(M):1.0(F). The Pearson’s chi-squared test (using Yates correction for continuity) revealed a P-value < 0.001, indicating that there was a highly significant difference in the observed sex frequency from a 1:1 expected Fisherian frequency, with male American crocodiles being significantly more numerous than females in the Ambergris caye population. The sex ratio of subadult males to subadult females in the Ambergris caye population was 1.16(M):1.0(F).

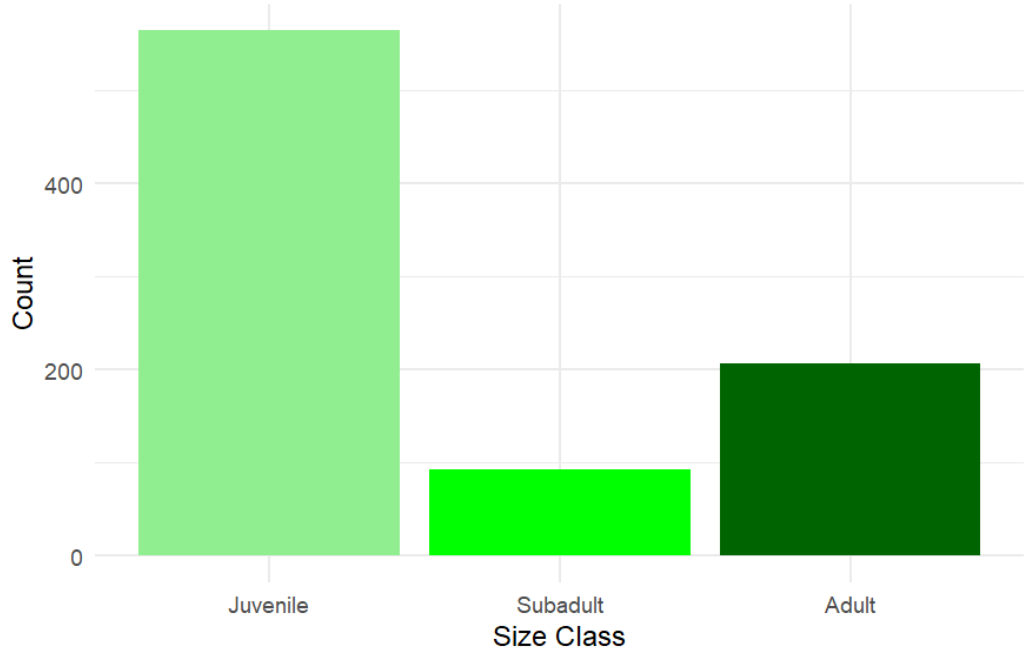

Figure. 4.7. The number of individuals captured and measured between 2011–2023 by ACES Wildlife Rescue in Ambergris caye, Belize. Categorisation follows Platt and Thorbjarnarson (2000b): Juvenile (TL<120 cm), subadult (TL=120-180 cm) and adult (TL>180 cm).

Crocodile morphometrics

Table 4.1 and Figure 4.8 summarize the morphometric data for all adult males (n=62), adult females (n=40), subadult males (n=31), subadult females (n=25), and juveniles (n=332) of American crocodiles captured on Ambergris caye and measured between 2011 and 2023.

Total Length (TL): The median TL for adult males was 244 cm, ranging from 181.1 cm to 365 cm. Adult females had a median TL of 222 cm, ranging from 182 cm to 310.8 cm. Subadult males and females have lower TL, with medians of 153.4 cm and 159.4 cm, respectively, and smaller intervals between lowest and highest values compared to adults. Median TL for juveniles ranged from 27.3 and 118.9 cm.

Snout Length (SL) and Head Length (HL): These measurements showed similar trends across age and sex, with adult males having the largest median values and juveniles the smallest.

Snout-Vent Length anterior (SVLa) and posterior (SVLp): These measurements also exhibit variations across groups, with adult males having the largest median SVLa and SVLp, followed by adult females, subadults, and juveniles. Sub-adults and juveniles show lower median values and narrower ranges compared to adults.

. For all measurements (TL, SL, DCL, SVLa, SVLp), data were found to be non-normal ($p < 0.001$), so non-parametric statistical tests were required for comparisons. Each group was compared independently as pairs using the Wilcoxon sum rank tests. The results of the Wilcoxon sum rank tests conducted to compare the Total Length (TL) among five groups: male adults, female adults, male

subadults, female subadults, and juveniles, indicate very highly significant differences ($p<0.001$) in TL between several pairs of groups, except between male sub-adults and female sub-adults where the difference was not significant ($p=0.9324$) (adult male median TL=244 cm, adult female median TL=222 cm, subadult male median TL= 153.4 cm, subadult female median TL =159.4 cm, juvenile median TL=76.25 cm).

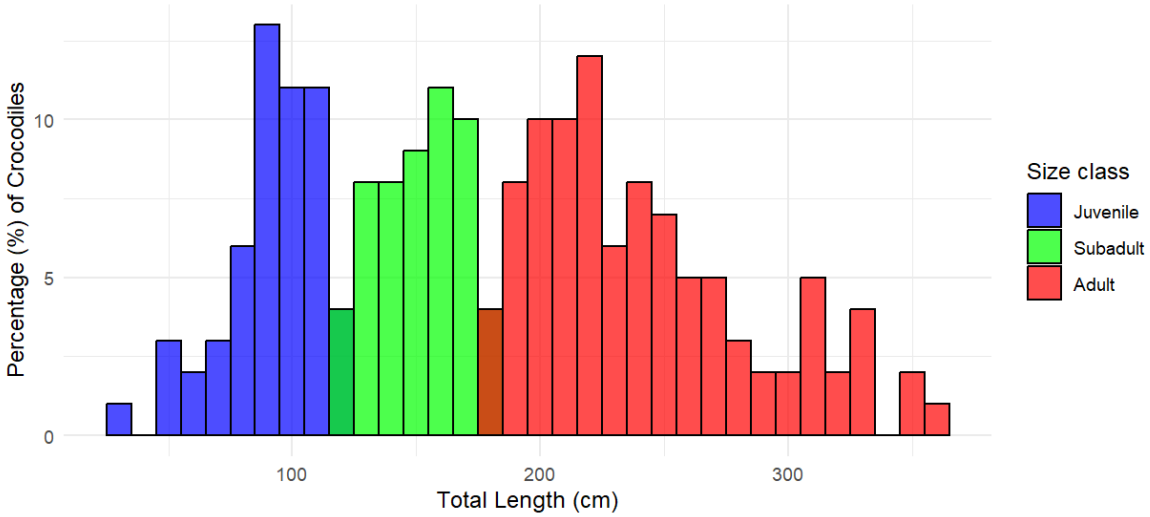

Figure 4.8. Size-frequency histogram for all individual American crocodiles (n=490) initial total length (TL), captured between 2011-2023 by ACES Wildlife Rescue in Ambergris caye.

Table 4.1. Biometric data summary for all adult male, adult female, subadult male, subadult female and juvenile crocodiles captured between 2011-2023 by ACES Wildlife Rescue in Ambergris caye.

(TL= total length; SL= snout length; DCL= dorsal cranial length; SVLa= snout vent length anterior; SVLp= snout vent length posterior).

	TL (cm)	SL (cm)	HL (cm)	SVLa (cm)	SVLp (cm)
			Adult Males (n=62)		
Median	244	25	36.5	117.95	124.9
Q1	209.125	21.55	31.4	102.3	107.5
Q3	287.825	29.5	42.6	133.9	148.7
Range	181.1 - 365	17.2 - 39.3	26.5 - 55	90-166	94.2 - 186.6
			Adult Females (n=40)		
Median	222	23	34.1	110.5	114
Q1	207.55	20.6	30.45	101.8	105.9
Q3	252.45	26.1	36.85	121.75	126.7
Range	182 - 310.8	17.6 - 33	26.3 - 49	87.5 - 153.3	90 - 159.7
			Subadult Males (n=31)		
Median	153.4	15.2	23.1	75	77.2
Q1	135.8	13.28	20.3	65.35	66.7
Q3	165.15	16.13	24.25	80.13	82.4
Range	121.5 - 180	11.1 - 18.9	17.8 - 27.9	50.4 - 92.3	54.5 - 98.2
			Subadult Females (n=25)		
Median	159.4	16.95	24.9	81.3	84.5
Q1	136.4	14.2	20.73	71.1	74.5
Q3	166	17.525	26.18	86.9	90.4
Range	121 - 180	11.4 - 25	15.5 - 35.5	61.2 - 115	63.7 - 120
			Juveniles (n=332)		
Median	76.25	7.6	12.6	41.3	42.8
Q1	55.3	6	10.13	33	34.35
Q3	91	9.2	14.7	47.3	49.25
Range	27.3 - 118.9	2.1 - 14	4.2 - 21.3	13.6 - 70.5	14.2 - 73.8

Sexual size dimorphism index (SDI)

In this study, an SDI value of 1.07 was computed for the species, indicating a slight bias towards larger males.

Growth rates

Of the 819 crocodiles captured over 13 years by ACES Wildlife Rescue, 296 were recaptures, allowing them to be used to calculate growth rates, however only a subset of them had their TL measured multiple times and could be used to determine growth rate. Growth rates could be calculated for 115 crocodiles (see Figure.4.9). Mean duration between capture and recapture was 806 ± 769 d (range: 25-3279 d). Of the 115 crocodiles, 47 were identified as male and 20 female, with the others (n=48) being too small to determine sex. Mean growth rate for TL was 0.045 ± 0.027 cm/d

(n=115) for all crocodiles, 0.048 ± 0.028 cm/d (n=47) for males and 0.039 ± 0.028 cm/d (n=20) for females (see Figure.4.9). For the 115 individuals, growth rates were highly variable among individuals, from minimum rates of 0.001 cm/d to maximum rates of 0.114 cm/d. By sex, minimum and maximum growth rates were 0.002 cm/d and 0.114 cm/d for males, and 0.001 cm/d and 0.109 cm/d for females, respectively.

The coefficient estimate for Mean_TL (-3.299e-05) was not statistically significant (p = 0.327) and did not show evidence of a significant linear relationship between growth rates and the mean TL of individuals (see Figure 4.9). The mean TL alone does not appear to be a significant predictor.

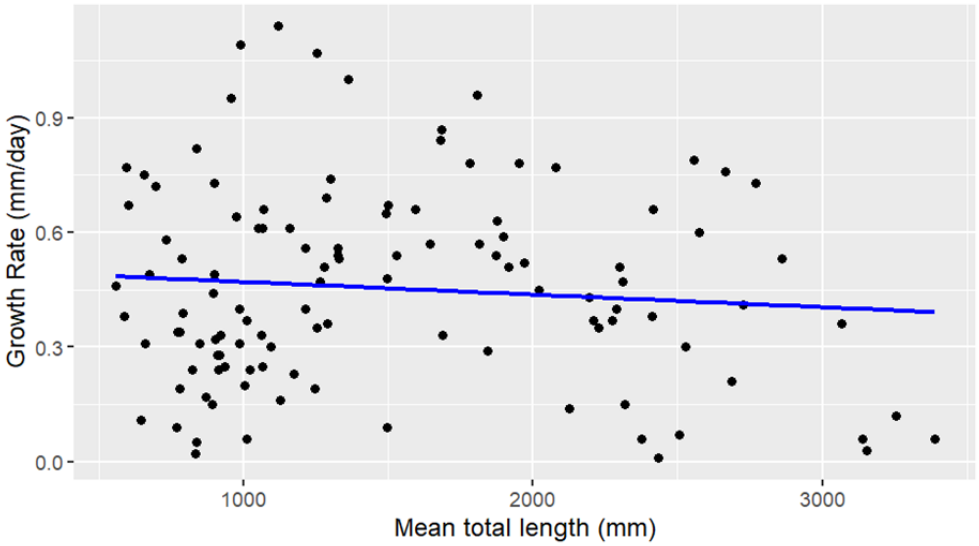

Figure 4.9. Relationship between growth rate of total length and mean total length between capture and recapture of 115 *Crocodylus acutus* from Ambergris caye, Belize.

The linear models fitted to male and female crocodiles reveal contrasting findings regarding the relationship between total length (TL) and growth rate. For male crocodiles, the model coefficients suggest a negligible and statistically insignificant association between TL and growth rate, with a p-value = 0.700. Furthermore, the model demonstrates poor fit, explaining only a minimal proportion of the variability in growth rates (adjusted R-squared = -0.01883). In contrast, the model for female crocodiles indicates a significant negative association between TL and growth rate, supported by a p-value = 0.00726. This model exhibits comparatively better fit, explaining approximately 30% of the variability in growth rates (adjusted R-squared = 0.3).

Both male and female growth rates were normally distributed. The Welch Two Sample t-test comparison of male and female growth rate did not find a statistically significant (t = -1.0925, p = 0.2819) difference. Based on the Welch Two Sample t-test, while the mean growth rate for females is lower than that for male there is no evidence to suggest a significant difference in growth rates between male and female crocodiles in the studied population (see Figure 4.10).

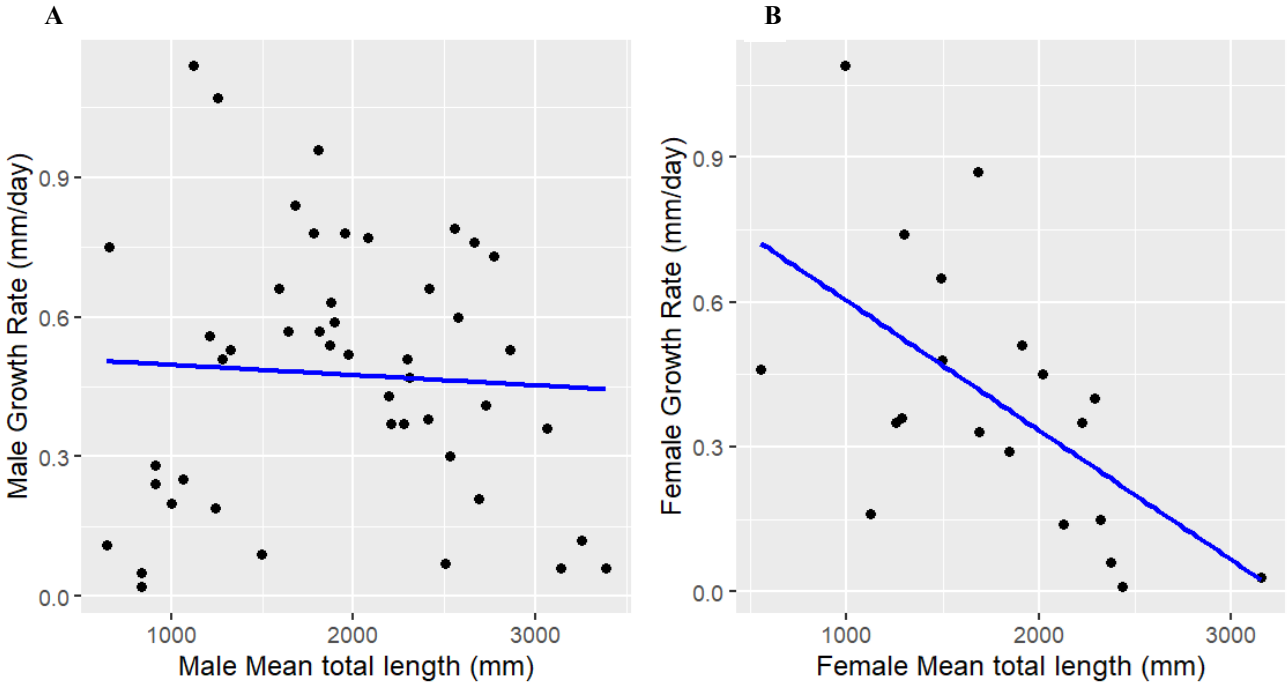

Figure 4.10. A: Relationship between growth rate of total length and mean total length between capture and recapture of 47 male *Crocodylus acutus* from Ambergris Caye, Belize. **B:** Relationship between growth rate of total length and mean total length between capture and recapture of 20 female Crocodylus acutus from Ambergris caye, Belize.

Morphometrics

Study results for adult male crocodiles in Ambergris caye (n=62) demonstrated strong correlations between the morphometric measurements (TL, SL, DCL, SVLa, SVLp). Table 4.2 summarises the various log-transformed allometric relationships between TL and SL, DCL, SVLa and SVLp. In the study of male adult crocodiles, strong correlations were observed between morphometric measurements and total length (TL). Notably, a negative allometric relationship was found between snout length (LogSL) and TL, indicating a slower rate of increase in snout length compared to TL. Similarly, dorsal cranial length (LogDCL) displayed a negative allometric correlation with TL, suggesting a slower rate of increase in head length compared to total body length. Snout-vent length anterior (LogSVLa) exhibited a negative allometric relationship. Conversely snout-vent length posterior (LogSVLp) displayed a positive allometric correlation with TL. Figure 4.11 shows log-transformed regressions between TL and the other measurements.

Adult female crocodiles in Ambergris caye (n=40) demonstrated strong correlations between TL aand the other morphometric measurements examined (TL, SL, DCL, SVLa, SVLp). Table 4.2 summarises

the various log-transformed allometric relationships between TL and SL, DCL, SVLa and SVLp. Notably, snout length (LogSL), dorsal cranial length (LogDCL), snout-vent length anterior (LogSVLa), and snout-vent length posterior (LogSVLp) exhibited robust positive correlations with TL, as evidenced by high R^2 values ranging from approximately 0.95 to 0.98. Additionally, all relationships demonstrated statistically significant associations with p-values less than 0.001. These findings suggest that these morphometric variables increase at a faster rate compared to total length, indicating positive allometric growth patterns in adult female crocodiles. Figure 4.12 shows log-transformed regressions between TL and the other measurements.

Subadult male crocodiles in Ambergris caye (n=31) demonstrated strong correlations between TL and the other morphometric measurements examined (TL, SL, DCL, SVLa, SVLp). Table 4.2 summarises the various log-transformed allometric relationships between TL and SL, DCL, SVLa and SVLp. In the examination of subadult male crocodiles, notably observed strong correlations in snout length (LogSL), head length (LogDCL), snout-vent length anterior (LogSVLa), and snout-vent length posterior (LogSVLp). LogDCL exhibited a robust positive correlation with DCL, showing an R^2 value of 0.81 and a statistically significant association (p-value < 0.001), indicative of negative allometric growth. Similarly, both LogSVLa and LogSVLp exhibited negative allometric relationships with TL, with R^2 values of 0.45 and 0.44, respectively, and p-values < 0.001. Conversely, LogSL displayed a positive allometric correlation with TL, with an R^2 value of 078. and a p-value < 0.001, indicating that head length increases at a faster rate compared to total length. Figure 4.13 shows log-transformed regressions between TL and the other measurements.

Subadult female crocodiles in Ambergris caye (n=25) demonstrated strong correlations between TL and the other morphometric measurements examined (TL, SL, DCL, SVLa, SVLp). Table 4.2 summarises the various log-transformed allometric relationships between TL and SL, DCL, SVLa and SVLp. In the examination of subadult female crocodiles, notably, dorsal cranial length (LogDCL), snout-vent length anterior (LogSVLa), and snout-vent length posterior (LogSVLp) displayed negative correlations with TL. LogSL exhibited an positive correlation with TL and had a R^2 value of 0.68 and a statistically significant association (p-value < 0.001), indicative of positive allometric growth, where snout length increases at a faster rate compared to TL. Conversely, LogDCL demonstrated negative allometric correlation with TL, with an R^2 value of 0.3 and a significant p-value < 0.001, suggesting that head length increases proportionately slower than TL. Likewise, both LogSVLa and LogSVLp showcased negative allometric relationships with TL, with R^2 values of 0.71 and 0.69, respectively, and p-values < 0.001. Figure 4.14 shows log-transformed regressions between TL and the other measurements.

Juvenile crocodiles in Ambergris caye (n=332) demonstrated strong correlations between TL and the other morphometric measurements examined (TL, SL, DCL, SVLa, SVLp). Table 4.2 summarises the

various log-transformed allometric relationships between TL and SL, DCL, SVLa and SVLp. For juveniles, snout length (LogSL), snout-vent length anterior (LogSVLa), and snout-vent length posterior (LogSVLp) exhibited robust positive correlations with TL. LogSL displayed a high R^2 value of 0.95 and a very low p-value (< 0.001), indicating a strong positive allometric relationship, where snout length increases at a faster rate compared to TL. Similarly, both LogSVLa and LogSVLp demonstrated substantial positive correlations with TL, with R^2 values of 0.95 and 0.95, respectively, and extremely low p-values (< 0.001), suggesting that both anterior and posterior snout-vent lengths increase proportionately faster than TL in juvenile crocodiles. Conversely, dorsal cranial length (LogDCL) exhibited a negative allometric correlation with TL, as evidenced by a high R^2 value of 0.94 and an exceptionally low p-value (< 0.001), indicating that head length increases at a slower rate compared to TL in juvenile crocodiles. Figure 4.15 shows log-transformed regressions between TL and the other measurements.

The DCL:CW ratio ranged from 2.7 to 4.2. The relationship between cranial width CW, DCL, and SVLp was investigated using a linear regression analysis. The analysis, revealed a coefficient estimate of 0.0015 (p = 0.195) for SVLp, indicating a weak and statistically insignificant relationship between the two variables. The adjusted R-squared value of 0.01722 suggested that the model explained only a small proportion of the variability in the DCL:CW ratio. Overall, the findings did not provide strong evidence to support a significant association between cranial morphology and body size in the crocodile population studied.

Table 4.2. Log-transformed allometric relationships between straight Total length (TL) and snout length (SL), dorsal cranial length (DCL), snout vent length anterior (SVLa) and snout vent length length posterior (SVLp) for American crocodiles in Ambergris caye.

Male Adult (n=62)	R^2	p-value	Growth
logSL = -2.0772 + 0.9671 * log TL	0.81	1.01E-18	Negative allometric
logDCL = -1.2195 + 0.8771 * log TL	0.83	9.30E-21	Negative allometric
logSVLa = 0.2945 + 0.8182 * log TL	0.74	6.26E-12	Negative allometric
logSVLp = -0.8234 + 1.0352 * log TL	0.88	1.98E-17	Positive allometric
Female Adult (n=40)	R^2	p--value	Growth
logSL = -3.5258 + 1.2335 * log TL	0.95	1.71E-22	Positive allometric
logDCL = -2.6168 + 1.1348 * log TL	0.95	1.60E-22	Positive allometric
ogSVLa = -1.0530 + 1.0671 * log TL	0.98	5.38E-23	Positive allometric
logSVLp = -1.0667 + 1.0760 * log TL	0.98	1.02E-22	Positive allometric
Subadult males (n=31)	R^2	p-value	Growth
logSL = -2.4473 + 1.0269 * log TL	0.78	1.16E-08	Positive allometric
logDCL = -1.4426 + 0.9108 * log TL	0.81	5.57E-09	Negative allometric
logSVLa = 0.1102 + 0.8362 * log TL	0.45	6.24E-04	Negative allometric
logSVLp = 0.2221 + 0.8217 * log TL	0.44	1.10E-03	Negative allometric
Subadult females (n=25)	R^2	p--value	Growth
logSL = -3.5465 + 1.2534 * log TL	0.68	7.46E-06	Positive allometric
logDCL = -1.1599 + 0.8554 * log TL	0.30	1.31E-02	Negative allometric
logSVLa = -0.9809 + 1.0637 * log TL	0.71	2.07E-05	Positive allometric
logSVLp = -0.8848 + 1.0512 * log TL	0.69	3.36E-05	Positive allometric
Juveniles (n=332)	R^2	p--value	Growth
logSL = -2.8605 + 1.1148 * log_TL	0.95	3.25E-114	Positive allometric
logDCL = -1.6623 + 0.9551 * log_TL	0.94	8.83E-121	Negative allometric
logSVLa = -0.7800 + 1.0211 * log_TL	0.95	1.60E-132	Positive allometric
logSVLp = -0.7400 + 1.0207 * log_TL	0.95	5.45E-127	Positive allometric

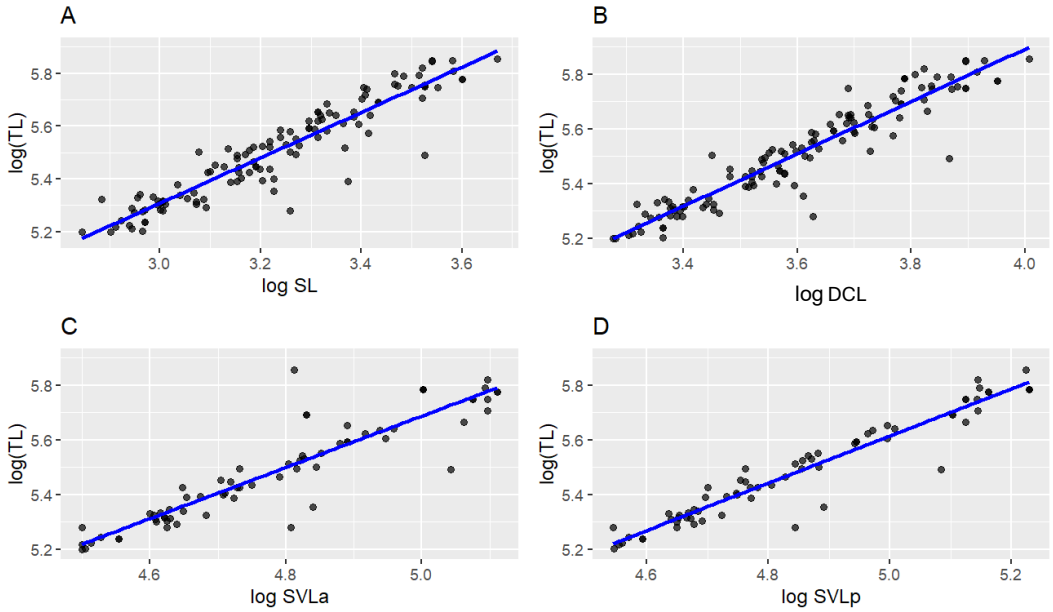

Figure 4.11. A; Relationship between log total length (TL) and the log of snout length (SL). **B;** Relationship between log total length (TL) and the log of dorsal cranial length (DCL). **C;** Relationship between log total length (TL) and the log of snout vent length anterior (SVLa). **D;** Relationship between log total length (TL) and the log of snout vent length posterior (SVLp). *Crocodylus acutus* adult males (n=62) Ambergris caye, captured between 2011-2023.

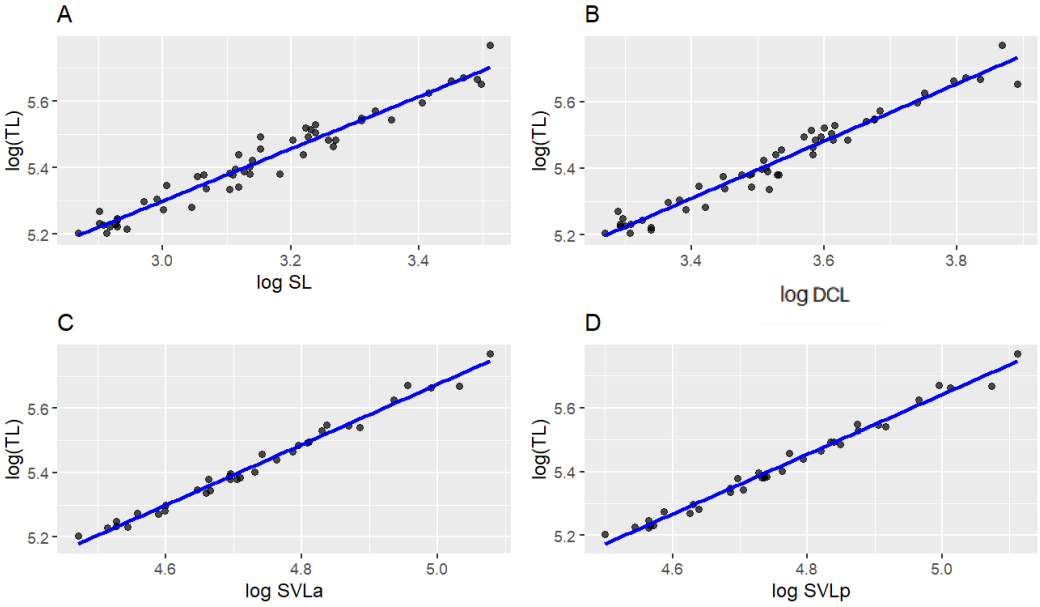

Figure 4.12. A; Relationship between log total length (TL) and the log of snout length (SL). **B;** Relationship between log total length (TL) and the log of dorsal cranial length (DCL). **C;** Relationship between log total length (TL) and the log of snout vent length (TL) and the log of snout vent length anterior (SVLa). **D;** Relationship between log total length (TL) and the log of snout vent length posterior (SVLp). *Crocodylus acutus* adult females (n=40) Ambergris caye, captured between 2011-2023.

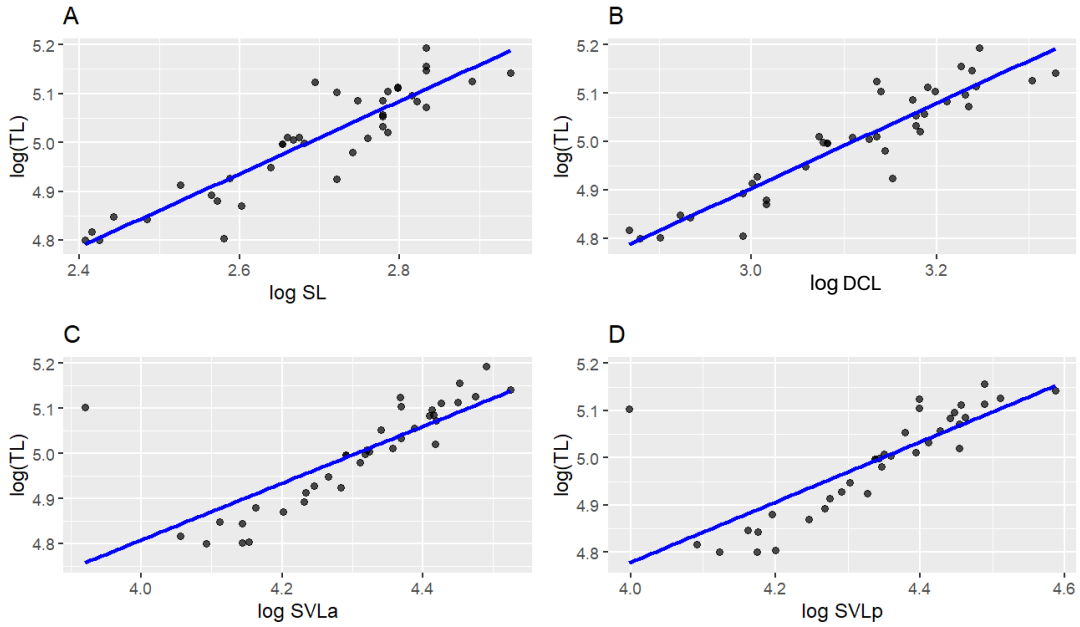

Figure 4.13. A; Relationship between log total length (TL) and the log of snout length (SL). **B;** Relationship between log total length (TL) and the log of dorsal cranial length (DCL). **C;** Relationship between log total length (TL) and the log of snout vent le length anterior (SVLa). **D;** Relationship between log total length (TL) and the log of snout vent length posterior (SVLp). *Crocodylus acutus* subadult males (n=31) Ambergris caye, captured between 2011-2023.

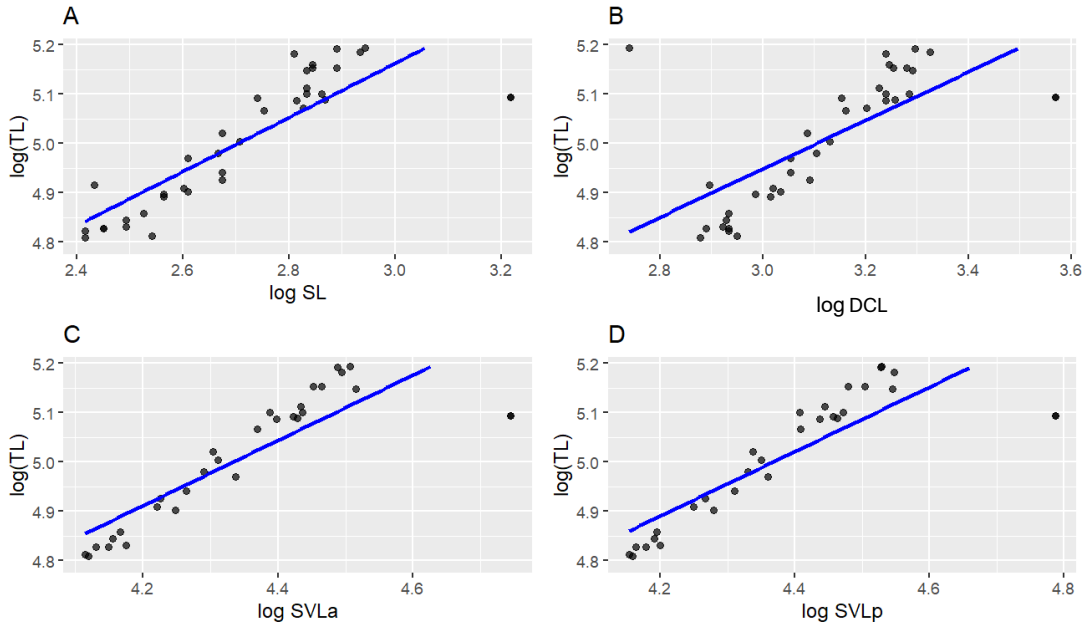

Figure 4.14. A; Relationship between log total length (TL) and the log of snout length (SL). **B;** Relationship between log total length (TL) and the log of dorsal cranial length (DCL). **C;** Relationship between log total length (TL) and the log of snout vent le length anterior (SVLa). **D;** Relationship between log total length (TL) and the log of snout vent length posterior (SVLp). *Crocodylus acutus* subadult females (n=25) Ambergris caye, captured between 2011-2023.

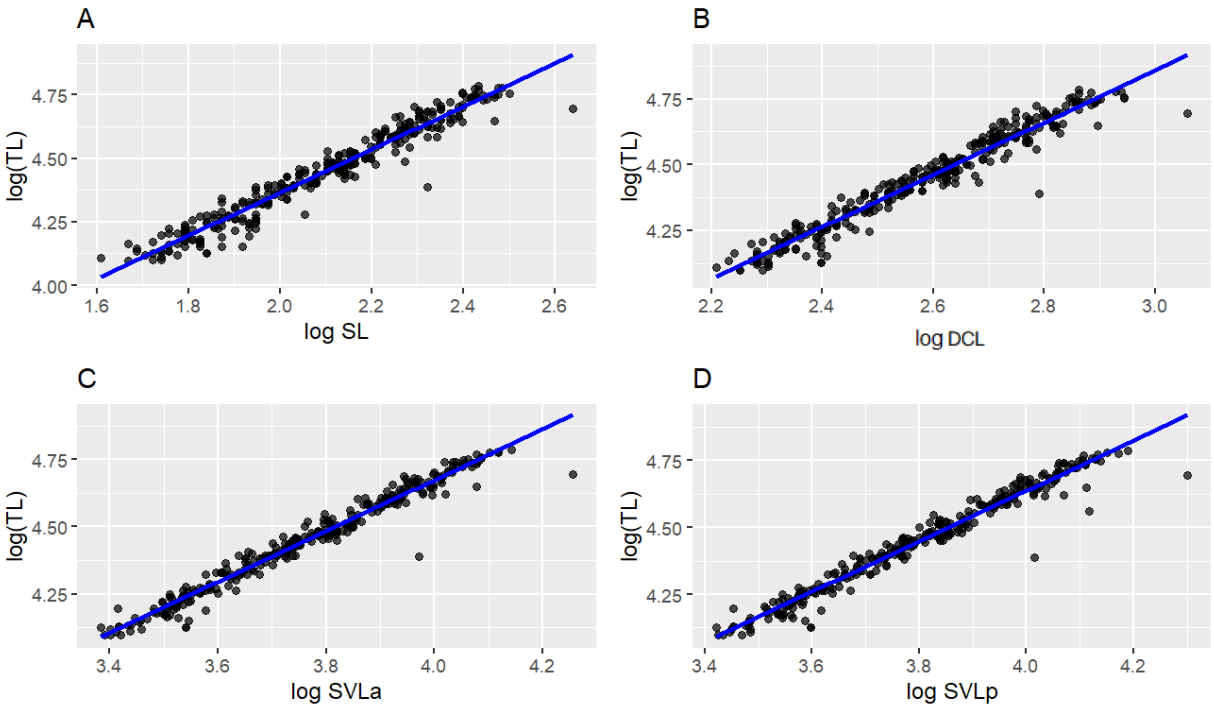

Figure 4.15. A; Relationship between log total length (TL) and the log of snout length (SL). **B;** Relationship between log total length (TL) and the log of dorsal cranial length (DCL). **C;** Relationship between log total length (TL) and the log of snout vent length anterior (SVLa). **D;** Relationship between log total length (TL) and the log of snout vent length posterior (SVLp). *Crocodylus acutus* juveniles (n=332) Ambergris caye, captured between 2011-2023.

Discussion

American crocodiles demonstrate varying degrees of sexual dimorphism across their range, with males typically larger, although populations in the Yucatan Peninsula exhibit a less pronounced size difference (Labarre et al., 2017). On Ambergris caye, adult males averaged a TL 19.75 cm longer than females, with a higher proportion of males (30) attaining lengths above 3 meters, including the largest individual recorded at 3.65 meters TL. In contrast, only two adult females exceeded 3 meters, with the largest measuring 3.2 meters long. This is similar to the maximum TL obtained by *C. acutus* in the Belizean part of the species range that have been previously confirmed (Platt and Thorbjaranson 2000b; Platt et al., 2011; Mauger et al., 2012).

The SDI calculated for American crocodiles in Ambergris caye was 1.07, a much smaller deviation from the common 20% size difference observed in other crocodilian species (Platt et al., 2009). This suggests a less pronounced sexual dimorphism in *C. acutus* compared with *C. niloticus* (2.19; Warner et al., 2016), *C. moreletii* (2.12; Platt et al., 2009) and *C. acutus* in the coastal zones of Belize (2.10,2.10; Platt et al., 2011, 2016). Past overharvesting of the Ambergris population may have contributed to the bias towards larger and/or older crocodiles being removed, potentially skewing the population's size structure (Platt and Thorbjarnarson, 2000b; 2000a). Consequently, larger crocodiles encountered today likely represent the first generations of population recovery, implying that the

reduced sexual dimorphism observed in the Ambergris caye population may not solely stem from differences in age structure between sexes (Charruau and Cedeño-Vázquez, 2005).Mean growth rate in length of *C. acutus* obtained in this study (0.045 ± 0.027 cm/d, n=115) was similar to that obtained in the Yucatan peninsula (Charruau et al., 2010; 0.044 ± 0.033 cm/d, n=27) and lower than that obtained in Oaxaca, Mexico (García-Grajales et al., 2012; ; 0.056 ± 0.049 cm/d, n=23) and Jalisco (Cupul-Magaña et al., 2004; 0.185 cm/d, n=124). This difference is likely because growth rate in length decreases with the increase in length of individuals in *C. acutus* (Charruau et al., 2010.; Garcia-Grajales, Buenrostro-Silva and Charruaua, 2012) as is seen in other crocodilian species (Webb et al., 1978; Hutton, 1987; Wilkinson and Rhodes, 1997).

In this study, hatchlings/yearlings and juveniles exhibited a growth rate in length averaging 0.057 cm/day, whereas the growth rate declined among adult crocodiles, averaging 0.035 cm/day. This may explain why the mean growth rate found on Ambergris caye is similar to the Yucatan (Charruau et al., 2010) as both of these studies included crocodiles of all size classes, while in Oaxaca (Garcia-Grajales, Buenrostro-Silva and Charruaua, 2012) and Jalisco (Huerta, Ponce Campos and Ross, 2002) growth rates were not obtained for adult individuals. Furthermore, growth rates obtained in the present study agree with those found in other studies (Thorbjarnarson, 1989; Mazzotti et al., 2007; Cherkiss et al., 2011). Throughout different life stages, growth rates exhibit a decelerating trend relative to TL, with juveniles demonstrating the highest growth rates, followed by subadults, and then adults. However, considerable variability in growth rates exists across all life stages and between sexes, likely attributable to environmental factors affecting metabolism, such as prey availability, salinity, temperature (Sebens, 1987; Heino and Kaitala, 1999; Mazzotti et al., 2019). Juveniles, being more susceptible to these environmental influences and less resilient to change (Charruau et al., 2022.; Garcia-Grajales, Buenrostro-Silva and Charruaua, 2010). display the greatest variability in growth rates. Nevertheless, the observed disparities in growth rates between sexes and life stages align with well-established patterns observed in crocodilians in general (Thorbjarnarson, 1996; Mazzotti et al., 2009; Balaguera-Reina et al., 2015).

In the present study, females exhibit a statistically significant decrease in growth rate as total length increases, potentially due to resource allocation towards reproduction after reaching sexual maturity. This trend, observed alongside sexual size dimorphism with males typically larger, suggests an anticipated higher growth rate in males (Platt et al., 2011). Though in the present study, while males had a higher average growth rate, it was not found to be statistically significant nor was there a strong relationship found between growth rate and total length, suggesting that growth rate in males, unlike in females, does not appear to slow as males total length increases. Other factors such as genetics, environment and social aspects factors can explain regional differences in mean growth rates of *C. acutus* (Garnett and Murray, 1986; Wilkinson and Rhodes, 1997; Tucker et al., 2007).

The notable disparity in the male-to-female sex ratio within the sample can be partially attributed to a bias favouring the capture of males, largely driven by their territorial behaviour. This bias is most pronounced among adult crocodiles, with a lesser yet still present bias toward males observed among sub-adults (Thorbjarnarnson, 1989). Additionally, sub-adults tend to avoid areas of potential predation and competition with adults. The population surveys conducted in Chapter 3 revealed a spatial distribution of crocodiles that aligns with this ontogenetic pattern, with regions characterised by dense adult populations exhibiting a lack of subadult individuals.

The observed bias towards capturing males may be further compounded by environmental factors that subject smaller adult males and sub-adults to heightened competition and exclusion from preferred habitats (Thorbjarnarson, 1989; Murray et al., 2015). This could result in these individuals coming into closer proximity with human settlements, thereby increasing the necessity for their capture and relocation. While this explanation sheds light on part of the observed bias towards males being captured.Given the island's small size and heavy development, it is plausible that such environmental pressures contribute to a higher proportion of males in the population. However, previous research on the male-to-female sex ratio of *C. acutus* in Belize did not identify this male bias, reporting an equal ratio (1:1) in Chenot-Rose (2013) and Tellez, Boucher, and Kohlman (2016). Furthermore, Platt et al. (2011) observed a female-biased sample with a ratio of 1:0.63. Future research efforts should explore the ratio of males to females on Ambergris caye and investigate potential underlying causes. It is worth noting that sex determination among *C. acutus* embryos, as with all crocodilians, is influenced by incubation temperature (Thorbjarnarson, 1996; Balaguera-Reina et al., 2015). Therefore, further exploration of the nesting ecology of the *C. acutus* population on Ambergris caye should investigate the influence of egg incubation temperatures on hatchling sex ratios, as well as sex-specific early life survival (Bock et al., 2023).

Crocodile growth patterns in Ambergris caye vary not only across sexes but also between different life stages. Adult males and females both exhibit positive allometric growth in snout length, suggesting a faster increase relative to total length. However, while head length and anterior snout-vent length demonstrate similar positive correlations with TL in adult females, adult males display a negative allometric relationship, indicating slower growth rates. Subadult males and females both exhibit mixed growth patterns, with snout length showing positive allometric growth, but head length and snout-vent length displaying negative allometric growth. Interestingly, juveniles demonstrate similar growth patterns to adult females, with positive allometric relationships observed in snout length and both anterior and posterior snout-vent lengths, but they diverge in head length, where juveniles exhibit negative allometric growth. These distinctions underscore the complexity of crocodile growth dynamics, influenced by both age and sex factors.

Crocodilian skull morphology is a result of a balance between hydrodynamics and biomechanical stress (Pierce, Angielczyk and Rayfield, 2008; Piras et al., 2014). Predominantly, crocodiles utilise a side swiping motion of the head to seize aquatic prey. Those with narrower or longer heads can employ this hunting strategy more effectively, making them better adapted to a primarily aquatic diet. However, as the skull narrows or elongates, bite strength diminishes (Pierce, Angielczyk and Rayfield, 2009). Intraspecific morphological diversity within a species is closely associated with prey characteristics such as size, speed, and hardness (Platt et al., 2006; Hanson et al., 2015).

Adult crocodiles inhabiting the offshore cayes and atolls of Belize primarily feed on hard-bodied crustaceans (Platt et al., 2013), although it remains uncertain whether this dietary preference extends to the Ambergris caye population. Tucker et al. (1996) proposed a general threshold for DCL:CW ratio in crocodilians, suggesting that broader skulls coincide with the ability to consume larger prey. The relatively broader skulls observed in the Ambergris caye population may facilitate the capture of larger prey compared to other regions within their range in Belize and the Yucatan Peninsula. The DCL:CW ratio observed on Ambergris caye (2.7 to 4.2) is higher than the range reported for other populations in the Yucatan peninsula (1.27 to 3.02) (Labarre et al., 2017). This suggests that crocodiles on Ambergris caye exhibit a similar but somewhat broader range of skull proportions compared to other populations. The DCL:CW ratio has been linked to dietary preferences in crocodilians, with broader skulls associated with larger prey consumption. The higher DCL:CW ratio on Ambergris caye suggests that crocodiles may consume a varied diet, potentially including larger prey items, compared to other regions within their range in Belize and the Yucatan Peninsula, but not to the extent observed in populations with even broader skulls. Further investigation into the diet of crocodiles on Ambergris caye would provide additional insights. The non-linear trends observed in the relationship between SVLp and DCL:CW are common in crocodilians (Strauss, 2012; Labarre et al., 2017).

Concluding comments

This study represents the first quantification of morphological characteristics within the American crocodile population inhabiting Ambergris caye. Notably, it constitutes one of the most extensive data sets utilised in a morphometric analysis of American crocodiles in Ambergris caye, Belize to date. This study is also the first investigation into growth rates of this species in Belize. The findings corroborate previous conjectures regarding population isolation contributing to morphological diversity, as documented by Charruau et al., (2010) and Labarre et al., (2017).The distinctive characteristics observed among the crocodile population on Ambergris caye appear to align with the site-specific environmental factors prevalent in the area, encompassing aspects such as prey availability, isolation, and habitat quality. Notably, the crocodiles on Ambergris caye exhibit a broader snouted morphotype reminiscent of island populations found along the Yucatan Peninsula. Although

hybridisation was considered as a potential factor influencing this morphology, recent genetic analyses conducted on this population indicate either minimal hybridisation or its absence altogether (Wilkie et al., 2024). Furthermore, the quantified growth rates support the notion of reduced sexual dimorphism, a phenomenon likely unrelated to the age structure of the population but rather indicative of historical overharvesting. These findings collectively contribute valuable insights into the population dynamics of American crocodiles in the Ambergris caye region.

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Chapter 5

Conclusions

This research highlights the presence of a stable population of American crocodiles on Ambergris caye, Belize, with active reproductive activity. Notably, the population has shown stability since its last comprehensive assessment in 2010-11 by Chenot-Rose (2013). The discovery of nine nests, among the highest reported nesting activities in the country, underscores the significance of the caye as a breeding ground. However, the population faces threats primarily stemming from the scarcity of suitable nesting habitat.

The extensive development of beach ridges on the caye has resulted in limited nesting areas, with instances of nest destruction and relocation due to hazardous conditions. Particularly concerning is the dependence of crocodiles on sewage treatment ponds as a primary nesting site, which exposes eggs and hatchlings to potential pollutants and habitat disruption if not managed appropriately. The current lack of vegetation surrounding the sewage ponds, where nesting occurs most frequently, exposes hatchlings to increased predation risk, particularly from avian predators. Encouraging the growth of native vegetation around the pond edges could potentially mitigate this vulnerability. However, any vegetation modification at the sewage pond site must strike a balance between crocodile survival needs and the operational requirements of the sewage ponds.

The data gathered during the six-month field study conducted in 2023, as well as analysis of the long-term dataset collected by ACES and the author, serves as a valuable baseline for future investigations and long-term monitoring efforts aimed at understanding temporal population dynamics. Given the importance of nesting success in population persistence, it is strongly recommended that future research monitor hatching success rates, with a focus on nests situated in the sewage ponds area. This can be achieved by deploying temperature and humidity data loggers within nest chambers to monitor crucial parameters and conducting mark-recapture of hatchlings. Additionally, research into recruitment rates and the viability of nesting at this site is imperative for informed conservation strategies. Furthermore, genetic assessment of the population to examine the possibility of hybridisation events, which could impact the genetic integrity of the population, is necessary.

A head-starting program could support Ambergris caye's American crocodile population in the short term by bolstering numbers and increasing the proportion of females. This conservation method, successfully applied to other crocodilian species (van de Ven et al., 2009), is controversial (Buitrago, Guada, and Doyle, 2008; Tetzlaff et al., 2019) and should be part of a broader strategy addressing species and habitat preservation. If implemented, the program should replicate natural conditions in captivity—encompassing microhabitats, diet, seasonal temperatures, and UV exposure—to minimize stereotypical behaviors and improve post-release survival. Adequate space, sanitation, and veterinary care are also essential to reduce mortality and prevent the release of compromised individuals. Additionally, juveniles raised in the program could be translocated to other suitable cayes and atolls in Belize, reinforcing regional crocodile populations.

Conservation efforts aimed at increasing the American crocodile population must carefully consider the potential impact on local communities. As large apex predators, American crocodiles can occasionally come into conflict with humans (García-Grajales and Buenrostro-Silva, 2019; Murillo and Cambronero, 2020; Pooley et al., 2021). While instances of predation on humans are rare, conflicts often arise due to predation on pets and livestock, as well as competition with fishing activities.

It is crucial to foster and maintain a positive attitude towards the species among local communities. This can be achieved by providing strategies for the removal or relocation of "problem" individuals, along with education initiatives and coexistence strategies. Emphasising the positive impact that American crocodiles can have for communities, such as their role in maintaining ecosystem balance, and highlighting the potential benefits of crocodile-related tourism are effective strategies for fostering a positive association with the species (Chirgwin and Harvey, 1999).

Incorporating education, outreach, and citizen science involvement of local communities as co-creators of research is vital for effective crocodile conservation efforts. Implementing educational programs and citizen science initiatives can raise awareness about the importance of crocodiles and their habitats while empowering locals to actively contribute to research and monitoring efforts. Collaborating with communities to develop conservation projects promotes sustainable solutions that benefit both people and crocodiles, while empowering locals as guardians of crocodiles and their habitats ensures long-term conservation success.

By addressing conflicts and promoting coexistence, conservation efforts can garner support from local communities, ultimately enhancing the success of crocodile conservation initiatives while also promoting human safety and well-being.

Habitat loss and degradation are recognized as primary drivers of population declines among many crocodilian species globally (de Vos, 1984; Thorbjarnarson et al., 2006; Lourenço-de-Moraes et al., 2023). The ongoing development of resorts and the expansion of urban areas, such as San Pedro town on Ambergris caye, have led to the transformation of landscapes into highly modified, human-dominated environments (Sweetman et al., 2019). This rapid and continuous development has undoubtedly altered crocodile habitats, although the precise impacts on the crocodile population remain largely speculative.

Protecting critical nesting habitat is imperative, as these areas are essential for carrying out vital life-history functions for the species (Camaclang et al., 2015). Additionally, conducting a comprehensive assessment of the crocodile population within the Bacalar Chico Marine Reserve and National Park (BCMRNP) is necessary. This entails locating and evaluating any nesting sites in the area and investigating movement patterns and dispersal from the southern regions of the caye to further north in Quintana Roo, Mexico, to ascertain the population's insularity or homogeneity.

The creation of artificial sand banks for nesting has yielded positive outcomes for American crocodile populations in other regions (Mazzotti, 1999). If considered, new nesting habitat should ideally be situated in locations that minimise disturbance to nesting females, be well-drained, easily accessible to female crocodiles, and incorporate varying levels of vegetational shading to promote thermal variability. Surveying BCMRNP to identify potential candidate sites is recommended in this regard.

Despite the positive outcomes of protective measures implemented in 1981 (creating the Wildlife Protection Act (WPA) chapter 220), the American crocodile population in Belize faces new challenges posed by expanding development and habitat loss. The potential resurgence of these threats continues to undermine much of the progress achieved in the species' recovery. Notably, the crocodile population on Ambergris caye remains relatively small and has not demonstrated growth over the past 13 years.

The findings of this study serve as a crucial resource for guiding policy decisions and informing the Belize Forest Department's efforts toward the development of a comprehensive management and recovery plan for the American crocodile. By incorporating the insights gained from this research, policymakers can formulate targeted strategies aimed at addressing current threats, preserving critical habitat, and ensuring the long-term viability of the crocodile population in Belize. Such proactive measures are essential for sustaining the positive trajectory of crocodile conservation for this species in the region.

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Appendix

FOREST DEPARTMENT

MINISTRY OF SUSTAINABLE DEVELOPMENT, CLIMATE CHANGE AND DISASTER RISK MANAGEMENT

FOREST DRIVE | TEL: 822-1524 | secretary@forest.gov.bz
BELMOPAN CITY | FAX: 822-1523 | www.forestdepartment.gov.bz

Ref. No. FD/WL/1/23 (17)
Ciaran O Mordha
University College Cork
College Rd,
County Cork.
Ireland

July 11th, 2023

SCIENTIFIC COLLECTION/RESEARCH PERMIT
WILDLIFE PROTECTION ACT NO. 14/2000

Permission is hereby granted to the above-named and address to do **Research/Collection** in the country of Belize subject to the following conditions:

1. The permit is:
   a) Valid for **Ciaran O Mordha only.**
   b) Valid until **July 10th, 2024**.

2. This permit provides research/collection to be done at: **Around Ambergris Caye.**
   NOTE: The above listed locations to be covered under this permit can only be accessed if the proper Scientific Collection/Research Permit from the Fisheries Department and permits from relevant government agencies is obtained which includes and approves the use of these area.

3. The permit allows the holders to do research entitled: **Population assessment of *Crocodylus actus* on Ambergris Caye.**

4. The objective of the research is to:
   a. **To assess population number and density of the American crocodile on Ambergris Caye.**
   b. **To determine the habitat and macrohabitat use of the spheres.**
   c. **To determine what habitats are of particular importance throughout the different life stages.**
   d. **To locate and determine sites of special importance for successful nesting of *C. acutus*.**

5. This permit provides for the following:
   a. **To conduct nighttime eyeshine surveys of different habitats and locations across the Caye using a GPS to mark out transects and to mark locations of animals spotted.**
   b. **To conduct Capture survey – noting where crocodiles are found by GPS; conduct standard health assessment to determine population makeup and distribution and tag using RFID for identification.**
   c. **To conduct Nest site location surveys locating nest sites during daylight hours in different location on the caye by skiff, golf cart or by foot.**
   d. **To conduct habitat monitoring – habitat usage, score areas where crocodiles are found based on primary habitat present, level of anthropogenic disturbance. Identify habitats used for nesting site selection.**

6. The permit holder must supply the Forest Department with **both digital and hard copies of final reports at the end of the project.**

7. This permit may be cancelled at any time not withstanding condition 1(b) above at the discretion of the Minister of Agriculture, Fisheries, Forestry, the Environment and Sustainable development.

8. The permit holder shall make provisions to accommodate Forest Department Staff on field trips as Convenient to both parties.

9. The permit does not grant permission to enter private/lease lands. Prior arrangements need to be made with land owners before entering any private/leased land.

10. Research fee has been paid vide Treasury Receipt No: **3988341** Dated: **11/07/2023**

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Figure A1: Belize Forest Department Research Permit.

11 August 2023

Private and Confidential

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Dear Ruth,

I can confirm that University College Cork's Animal Experimentation Ethics Committee has approved the Animal Ethical Review Request (#2023-017) for your project titled: "Population assessment of *Crocodylus actus* around Ambergris Cave."

Please note this approval only applies to this specific project and is subject to you holding, if required, authorisation and/or local permits to undertake this programme of work.

Yours sincerely,

Professor Christian Waeber
Chair, AEEC Committee &
AEEC review sub-committee

Professor Christian Waeber
Chair, AEEC Committee & AEEC review sub-committee
Ollscoile na hÉireann, Corcaigh
National University of Ireland, Cork

Figure A2: University College Cork ethical approval for the capture of crocodiles for data collection.

Supplementary Material to Chapter 3

Figure A3.1: *Crocodylus acutus* nest located underneath burn pit, Ambergris caye, Belize, 2023 Souece: Ciarán Ó Mórdha

Figure A3.2: *Crocodylus acutus* nest located at the Sewage Ponds, Ambergris caye, Belize, 2023. Source: Ciarán Ó Mórdha.

Figure A3.3: *Crocodylus acutus* adult swimming in the sewage pond, Ambergris caye, Belize, 2023. Source: Ciarán Ó Mórdha.

Figure A3.4: Club Cart CarryAll 1500 UTV, used for crocodile surveying. Source: Ciarán Ó Mordha.

Figure A3.5: 19.6ft Carolina Skiff with a 40hp Yamaha four stroke outboard used for crocodile surveying. Source: Ciarán Ó Mordha.

Supplementary Material to Chapter 4

Figure A4.1: Biometric measurements of adult *Crocodylus acutus,* Ambergirs caye, Belize, 2023. Source: Ciarán Ó Mórdha.