LANDSCAPE GENETICS AND HABITAT VIABILITY OF THE ESTUARINE CROCODILE (*CROCODYLUS POROSUS*) IN SABAH: CONSERVATION MANAGEMENT OF AN APEX PREDATOR

SAI KERISHA KNTAYYA

Organisms and Environment Division
School of Biosciences
Cardiff University

A thesis submitted to Cardiff University in accordance with the
requirements for the degree of Doctor of Philosophy
in the School of Biosciences, Cardiff University

December 2024

ABSTRACT

The estuarine crocodile (*Crocodylus porosus*), an apex predator and an integral component of Sabah's biodiversity, faces increasing pressures from habitat loss, human-wildlife conflict, and environmental changes. This thesis provides a comprehensive study of *C. porosus* populations in Sabah, integrating demographic, genetic, spatial, and viability analyses to inform effective conservation strategies. Surveys conducted across 10 rivers revealed variability in population densities and size-class distributions, with fragmentation limiting genetic flow among populations. Spatial movement analyses, using GPS telemetry, highlighted sex-specific differences in home range patterns, the importance of oxbow lakes and tributaries as critical habitats, and potential avoidance of anthropogenic structures such as bridges. Genetic analysis of 100 tissue samples using 16S, CytB, ND2 and D-loop markers revealed that while the overall genetic diversity of *C. porosus* in Sabah remains high, individual river populations exhibited low diversity, with the Paitan River identified as a genetic hotspot. Population Viability Analysis (PVA) simulations using Vortex projected that the overall metapopulation could persist over the next century, but this is heavily dependent on the Kinabatangan River population. Many smaller river populations, including those in Padas and Labuk, showed alarming trends toward decline or local extinction, emphasizing the need for targeted conservation efforts. The findings stress the importance of habitat restoration, enhancing connectivity, and managing human-crocodile conflict to support population recovery and sustainability. Additionally, the thesis highlights the need for non-lethal strategies to mitigate conflict and the development of wildlife-friendly infrastructure to reduce habitat fragmentation. By synthesizing insights across ecological, genetic, and spatial scales, this research provides a robust framework for understanding and managing *C. porosus* populations in Sabah. The results underline the critical role of habitat quality, genetic diversity, and ecological connectivity in ensuring the long-term viability of this species. This thesis offers actionable recommendations for conservation, aiming to preserve *C. porosus* as a vital component of Sabah's unique biodiversity and a key contributor to the ecological balance of its riverine ecosystems.

ACKNOWLEDGEMENT

First and foremost, I extend my deepest gratitude to my supervisor, Benoit Goossens, for his unwavering support and guidance throughout my study. Your encouragement and gentle push have been invaluable. To my co-supervisor, Pablo Orozco Ter-Wengel, thank you for your academic advice and for patiently guiding me through statistics, shaping this work with your expertise. I am also grateful to the DGFC family, past and present, for your support, friendship, and shared expertise whether in the field, lab, or office. My heartfelt appreciation also goes to everyone at the Sabah Wildlife Department for their pivotal support in logistics, technical assistance, and administration.

I am sincerely grateful to my family, whose unwavering support has been the foundation of this journey. To my mother, Pauline, your boundless emotional strength and your selfless care for the children allowed me the focus and determination to pursue this work. I can never thank you enough, Ma. To my father, Kntayya, who has been my constant source of academic inspiration and a role model in every sense. Pa, it is because of your guidance and example that I embarked on this journey, and if I achieve even a fraction of what you have, I will consider myself truly fortunate. To my sister, Brindha, thank you for simply being the best sister I could ask for. To my in-laws, Kishore and Rita, thank you, mom and dad, for your faith in me and for always being there to lend a helping hand with the children whenever I needed it.

To my relatives and friends who have journeyed along with me these past seven years, thank you for the kind words, laughter, and occasional distractions that provided me with the balance I needed during this intense journey. You all know who you are.

To my husband, Kunal, I am utterly grateful for your encouragement, your patience and belief in me, and above all, your enthusiasm for what I am most passionate about – animals and nature. Thank you for always being proud of what I do and for sharing this journey with me.

To my two greatest achievements, Tiya and Navya, thank you both for making me a mother during this PhD journey. Although it has been challenging, I have cherished every moment. Your smiles and warm hugs after long days of work have been my greatest source of strength. One day, I hope you both read this and understand that you both are, and always will be, my proudest achievements. This PhD is for you both, to inspire you to strive for excellence and to follow your dreams.

Finally, I want to thank God, my Guru, Swami for all that I am and for all that I'm blessed with.

Contents

List of Tables

List of Figures

CHAPTER 1

Introduction & Literature Review

Wildlife conservation has become an urgent global priority as biodiversity faces increasing threats from human activities. Habitat loss, climate change, overexploitation, and pollution are key drivers pushing numerous species toward extinction (Pimm *et al*., 2014). Apex predators, in particular, play a critical role in maintaining the balance of ecosystems, yet they are often among the most vulnerable due to their reliance on large habitats and prey availability (Estes *et al*., 2011). Effective conservation strategies are essential not only for the survival of individual species but also for the preservation of entire ecosystems and the services they provide to humanity (Cardinale *et al*., 2012).

In tropical regions like Southeast Asia, rapid urbanization and deforestation have drastically altered landscapes that were once rich in biodiversity (Sodhi *et al*., 2010; Wilcove *et al*., 2013). Coastal and riverine ecosystems, in particular, have experienced significant habitat degradation, threatening wildlife species that rely on these environments (Hughes, 2017). Protected areas have been established in many regions, yet the implementation and enforcement of conservation laws remain challenging (Laurance *et al*., 2012). As a result, wildlife populations continue to decline, highlighting the need for comprehensive management plans that include habitat restoration, species monitoring, and community engagement (Brooks *et al*., 2006; Bennett *et al*., 2017).

Successful wildlife management requires a multi-faceted approach, incorporating ecological, social, and economic considerations (Lindenmayer & Likens, 2010; Redford *et al*., 2011). For species with wide-ranging habitats, like many large reptiles and mammals, understanding movement patterns and habitat use is crucial for identifying key conservation areas (Tucker *et al*., 2018). Conservationists have increasingly turned to technological advancements such as satellite tracking and camera trapping to monitor wildlife populations and gather data on behavior (Kays *et al*., 2015). This data not only informs management plans but also helps to mitigate human-wildlife conflicts, a growing concern as human populations expand into previously uninhabited areas (Dickman, 2010).

In addition to ecological research, wildlife management often involves collaboration with local communities (Berkes, 2004). Many species, especially apex predators, are perceived as threats to human livelihoods, leading to conflicts that can hinder conservation efforts (Inskip & Zimmermann, 2009). Educating communities about the ecological importance of such species and promoting sustainable land-use practices are essential for long-term conservation success (Treves *et al*., 2009). In many regions, including parts of Southeast Asia, community-based conservation programs have proven effective in reducing poaching and habitat destruction (Brooks *et al*., 2013).

The conservation of apex predators is particularly important due to their role as keystone species (Paine, 1969). They regulate the populations of prey species, maintaining a healthy and well-balanced, functioning ecosystem (Ripple *et al*., 2014; Sergio *et al*., 2008). However, due to their size, resource needs, and slow reproduction rates, apex predators are especially vulnerable to environmental changes and human interference (Cardillo *et al.*, 2005). Hence, safeguarding their survival needs long-term, adaptive management strategies that address both current threats and future challenges (Hunter *et al*., 2010).

1.1 Crocodilians

Crocodilians are inhabitants of tropical and subtropical aquatic habitats and are known to be prominent and widespread in their ecosystem. This group is implicated in positive effects in their environments as 'keystones species'. They sustain ecosystem structure and function through activities such as selective predation on fish species, recycling nutrients and maintaining wet refugia during the drought (King, 1988). There are currently 24 extant species of crocodilians that (Hekkala *et al*., 2011) (Table 1.1). They exhibit widespread diversity of size, habitat, diet preference, reproductive behavior, and many other biological aspects However, all species have certain similar aspects of life such as being effective aquatic predators. Aquatic insects, small fish and crustaceans often fall prey to them at early stages of their life. As they grow, they turn to vertebrates such as fish, turtles, birds and mammals for food.

Crocodilians regulate their body temperature by basking in the sun when cold and resting under the shade when hot (Seebacher *et al.,* 2003; Grigg & Kirshner, 2015). Their metabolism rate is highly efficient, they have extremely fast reflexes, and they possess effective locomotive skills both on land and in water (Webb & Manolis, 1989). Crocodilians also exhibit complex behaviours, including social interactions, dominance hierarchies, vocalization, and sophisticated maternal instincts (Campbell, 1973; Lang, 1987). Wild crocodilians are relatively long-lived, with some individuals living up to 70 years in the wild (Grigg & Kirshner, 2015).

Female crocodilians lay between 10 to over 60 eggs into a hole dug in the ground or into a mound of vegetation (Magnusson, 1982). Most females remain near their nest throughout the incubation period to protect it from predators (Joanen & McNease, 1971). After hatching, the hatchlings remain with the mother for several months, during which a large number die due to predation by other animals, including other crocodilians (Thorbjarnarson, 1996). The surviving individuals reach adulthood between the ages of five and 15 years, with females growing at a slower rate and reaching maturity at a smaller size than males (Webb & Manolis, 1989).

Table 1.1. Taxonomic Classification of Extant Crocodilian Species

Class Reptilia	
Order Crocodilia	
Family Alligatoridae (alligators & caimans)	
American Alligator	*Alligator mississippiensis*
Chinese Alligator	*Alligator sinensis*
Black Caiman	*Melanosuchus niger*
Broad-snouted Caiman	*Caiman latirostris*
Spectacled Caiman	*Caiman crocodilus*
Yacare Caiman	*Caiman yacare*
Cuvier’s Dwarf Caiman	*Paleosuchus palpebrosus*
Schneider’s Smooth-fronted Caiman	*Paleosuchus trigonatus*
Family Crocodylidae (true crocodiles)	
African Slender-snouted Crocodile	*Mecistops cataphractus*
American Crocodile	*Crocodylus acutus*
Australian Freshwater Crocodile	*Crocodylus johnstoni*
Cuban Crocodile	*Crocodylus rhombifer*
Dwarf Crocodile	*Osteolaemus tetraspis*
Morelet’s Crocodile	*Crocodylus moreletii*
Mugger Crocodile	*Crocodylus palustris*
New Guinea Freshwater Crocodile	*Crocodylus novaeguineae*
Nile Crocodile	*Crocodylus niloticus*
West African Crocodile	*Crocodylus suchus*
Orinoco Crocodile	*Crocodylus intermedius*
Philippine Crocodile	*Crocodylus mindorensis*
Saltwater Crocodile	*Crocodylus porosus*
Siamese Crocodile	*Crocodylus siamensis*
Family Gavialidae (gharial & tomistoma)	
True Gharial/Indian Gharial	*Gavialis gangeticus*
False Gharial/Malayan Gharial	*Tomistoma schlegelii*

Crocodiles, alligators, caimans, and gharials are all members of the order Crocodylia, but they exhibit distinct morphological differences that help differentiate them (Figure 1.1). One of the most noticeable differences is in the shape of their snouts. Crocodiles have a V-shaped, pointed snout, which is adapted for catching a variety of prey, including fish and mammals (Grigg & Kirshner, 2015). Alligators and caimans on the other hand, possess broader, U-shaped snouts that are well-suited for crushing prey like turtles and other hard-shelled animals (Webb & Manolis, 1989). Caimans, which are a subgroup within the alligator family, share similar snout structures but tend to be smaller and exhibit more jagged, ridged skin (Thorbjarnarson, 1999).

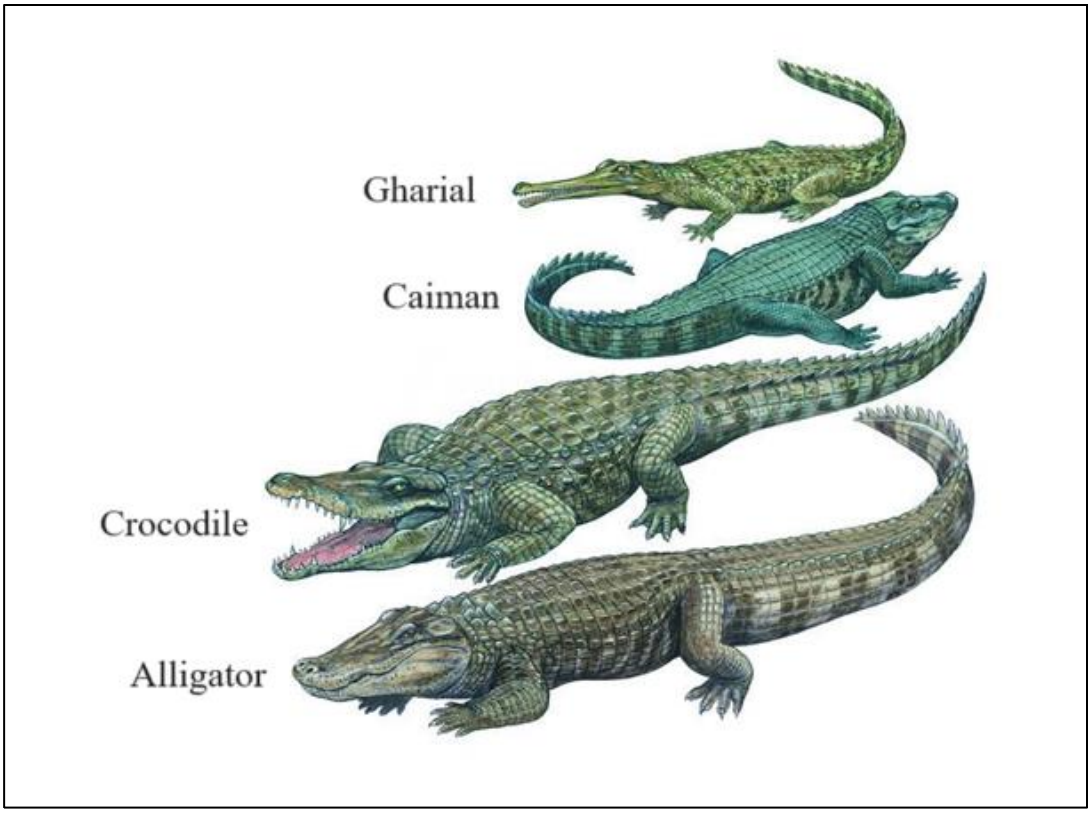


Figure 1.1. Size comparison between Gharial, Caiman, Crocodile and Alligator (Price, 2017)

Gharials are easily distinguishable from other crocodilians by their long, narrow snouts, lined with sharp interlocking teeth that aid in their piscivorous diet (Stevenson & Whitaker, 2010). Additionally, while crocodiles and alligators have visible teeth when their mouths are closed, gharial teeth are highly visible at all times due to the narrowness of their snouts (Britton, 2012).

Other morphological differences include the positioning of the salt glands. Crocodiles have functioning salt glands on their tongues, allowing them to thrive in brackish and saltwater environments, whereas alligators and caimans lack fully developed salt glands, restricting them mostly to freshwater habitats (Taplin & Grigg, 1989). Gharials are restricted to freshwater river systems due to their specialized ecological needs.

Although crocodiles, alligators, caimans, and gharials are morphologically distinct, they face the same conservation concern due to their distinct natural history. As apex predators, they play an essential role in their ecosystems, but they are often perceived as a threat to humans and livestock (Thorbjarnarson, 1992; Pooley, 2016). Despite their crucial ecological function, they are highly vulnerable to habitat destruction and alteration. The loss of any crocodilian species would represent a significant blow to biodiversity, economic benefits, and ecosystem stability (Webb & Manolis, 1989). Overexploitation for their valuable skin continues to support an international trade valued at over US$500 million annually (Ross, 1998). Historically, unchecked commercial exploitation and indiscriminate killing led to severe population declines and reduced species distribution. While no crocodilian species has become extinct solely due to direct human exploitation, the combination of overharvesting and habitat loss has driven several species to the brink of extinction (Hutton & Webb, 1992).

Crocodilians are reliant on aquatic habitats, although different species demonstrate varied habitat preferences. They thrive in tropical and subtropical wetlands, such as rivers, lakes, lagoons, mangroves, and marshes, with some species even venturing into marine environments (Thorbjarnarson, 1999). Due to their large size and continuous growth, crocodilians require extensive and diverse habitats to sustain viable populations. While most species need large, undisturbed areas, some, such as the common caiman (*Caiman crocodilus*) and Chinese alligator (*Alligator sinensis*), have shown resilience in adapting to smaller, fragmented habitats (Wu *et al*., 2002).

Habitat destruction remains the primary threat to crocodilian survival, with deforestation, agricultural expansion, and pollution being the most significant drivers of habitat loss (Webb *et al*., 2010). Smaller-scale habitat alterations can also have detrimental effects, especially in specific ecosystems. For example, female saltwater crocodiles in the Andaman Islands rely on limited freshwater marshes for nesting. These areas, however, are increasingly converted for agricultural purposes, leading to human-crocodile conflicts and mortality. Even though large stretches of riverine and mangrove habitats remain untouched, the loss of critical nesting sites contributes to population declines in the region (Whitaker & Whitaker, 2008).

In countries like the Philippines, rural communities living along rivers depend heavily on them for their daily livelihood, utilizing these water bodies for transport, fishing, and washing (Banks, 2005). Despite seemingly intact riverine habitats and low human occupancy in many areas, the constant killing of crocodiles has led to the depletion of both the Philippine crocodile (*Crocodylus mindorensis*) and saltwater crocodile populations (van Weerd & van der Ploeg, 2012). Similarly, in Malaysia, many rural people coexist with crocodiles, acknowledging their presence and sharing the rivers with them (Ibrahim *et al.*, 2010). In contrast, in Florida, indirect environmental factors such as river contamination from mercury and pesticides have been linked to reproductive issues in crocodilian species, which further obstructs their population growth (Rainwater *et al*., 2002; Roche *et al*., 2009).

Overall, the proximity and density of human populations are significant factors contributing to the vulnerability of crocodilian populations (Woodward *et al.*, 2010). At the same time, many crocodilian species exhibit ecological robustness, adapting to environmental changes as long as they have adequate prey and nesting sites (Webb & Manolis, 1989). Therefore, the survival of crocodilian populations in any region heavily depends on creating incentives to maintain these species and their habitats in a relatively undisturbed state (Thorbjarnarson, 1999).

1.2 The Estuarine Crocodile

The estuarine crocodile, often referred to as the saltwater crocodile, Indo-Pacific crocodile, marine crocodile, or sea crocodile, and conversationally as “salties”, boasts a long and fascinating evolutionary history dating back to the Cretaceous period, approximately 100 million years ago (Salisbury & Willis, 1996). This species is part of the Crocodylidae family, which includes all true crocodiles (Brochu, 2003). Fossil records suggest that the ancestors of modern estuarine crocodiles were widespread across what is now Africa, Europe, and Asia (Martin & Benton, 2008). Over millions of years, these ancient crocodiles adapted to various environmental conditions, leading to the diverse range of crocodilian species we see today. The estuarine crocodile evolved to thrive in coastal and estuarine environments, developing physiological adaptations that allow it to inhabit both freshwater and saltwater ecosystems (Webb & Manolis, 1989).

Historically, estuarine crocodiles had a widespread distribution across Southeast Asia, Northern Australia, the eastern coast of India, and extending as far west as the eastern coast of Africa (Webb & Manolis, 1989; Whitaker & Whitaker, 2008). These powerful reptiles have been revered and feared by indigenous cultures for centuries, often featuring prominently in local myths and legends. In Australia, for example, Aborigines have long respected the estuarine crocodile as an ancestral being (Langton, 2008). Despite their historical abundance, estuarine crocodile populations faced dramatic declines due to extensive hunting and habitat loss during the 19th and 20th centuries (Ross, 1998; Read*.,* 2004). However, intensive conservation efforts, particularly since the 1970s, led to the recovery of some populations, though the species remains vulnerable in many parts of its range (Britton, 2012; Campbell *et al.,* 2013).

The estuarine crocodile is classified as the largest of all living crocodilians, with reported lengths of up to seven meters (Webb & Manolis, 2009). On average, adults grow up to 3.50 – 4.50 m in length (Brazaites, 1974). It is differentiated from other crocodile species by its larger size and is part of one of the oldest lineages in the world (Caldicott *et al*., 2005). It is renowned for its distinctive morphology, which has evolved to make it one of the most formidable predators in both freshwater and marine environments. Adult males can reach lengths of up to 7 meters (23 feet) and weigh over 1,000 kilograms (2,200 pounds), making them the largest living reptiles (Britton, 2012). Their robust, elongated bodies are covered in tough, armour-like scales, which provide protection and aid in thermoregulation. The dorsal surface is typically greyish-brown with darker mottling, while the ventral surface is lighter, often yellowish, which may serve as camouflage in different aquatic environments (Webb & Manolis, 1989).

The head of the estuarine crocodile is particularly adapted for its predatory lifestyle. It has a broad, powerful snout that houses an impressive array of teeth, with 64 to 68 teeth in total, designed for gripping and tearing flesh (Campbell *et al.*, 2013). The placement of the eyes, ears, and nostrils on the top of the head allows the crocodile to remain almost completely submerged while stalking prey, providing a stealth advantage. The eyes possess a vertical slit pupil, which enhances night vision, and are equipped with a nictitating membrane that protects the eyes underwater (Grigg & Kirshner, 2015). This combination of features makes the estuarine crocodile an efficient ambush predator, capable of sudden, explosive movements to capture prey.

The estuarine crocodile's limbs and tail further contribute to its aquatic capabilities. The limbs are relatively short but strong, with webbed hind feet that aid in swimming. The powerful tail, which constitutes nearly half the animal’s length, is laterally compressed and acts as the main propulsive force in the water (Grigg & Kirshner, 2015). On land, the crocodile uses its limbs to engage in a high walk, where the body is lifted off the ground, allowing it to traverse considerable distances. This combination of morphological adaptations not only facilitates efficient movement in both water and on land but also underscores the estuarine crocodile's status as a top predator across diverse habitats.

The estuarine crocodile has the most extensive distribution of any living crocodilian species, spanning diverse aquatic habitats across several continents. This species is native to the coastal regions and river systems of Southeast Asia, Northern Australia, and the eastern coast of India, extending westward to the eastern coast of Africa. In Southeast Asia, estuarine crocodiles are found in countries such as Indonesia, Malaysia, the Philippines, Papua New Guinea, and the Solomon Islands (Webb & Manolis, 1989). These regions offer a variety of suitable habitats, including estuaries, mangroves, rivers, and coastal lagoons, where the crocodiles can thrive.

In Malaysia, there is historical evidence that points to the existence of another species, *Crocodylus raninus*. The earliest scientific record of this species dates back to 1844, when Müller and Schlegel described *C. raninus* based on adult and juvenile skulls believed to have come from Pontianak, West Kalimantan, Borneo. Ross (1990) also identified a *C. raninus* specimen collected by William T. Hornaday in 1878. However, the taxonomic status of *C. raninus* in Borneo has been controversial, with surveys in 1995 and 1996 failing to find definitive materials, although some specimens from a crocodile farm in Pangkalanbun, Central Kalimantan, were believed to belong to the *raninus* group (Ross *et al*., 1998). Additionally, Das and Charles (2000) identified a juvenile *C. raninus* skull from Tasek Merembun, Brunei Darussalam. In contrast, the only recorded specimen of *C. siamensis* in Malaysia was noted by Smith (1919) from Peninsular Malaysia, with no documented records from Sarawak or Sabah (Sebastian, 1993).

In Northern Australia, the estuarine crocodile is commonly found in the coastal regions of Queensland, the Northern Territory, and Western Australia. Australian populations are well-documented, with significant efforts made to monitor and manage these apex predators, particularly in areas where their habitats overlap with human activities (Britton, 2012). The species has been reported to utilize both freshwater and marine environments, with individuals often traveling long distances across open seas to colonize new territories. This ability to traverse vast stretches of ocean contributes to the species' wide distribution and genetic exchange between populations in different regions.

Further west, estuarine crocodiles are present along the eastern coast of India and Sri Lanka, where they inhabit tidal rivers, estuaries, and coastal swamps. They have also been reported in parts of Bangladesh and Myanmar, highlighting their adaptability to various environmental conditions (Groombridge, 1987). The distribution of estuarine crocodiles is influenced by several factors, including habitat availability, salinity tolerance, and prey abundance.

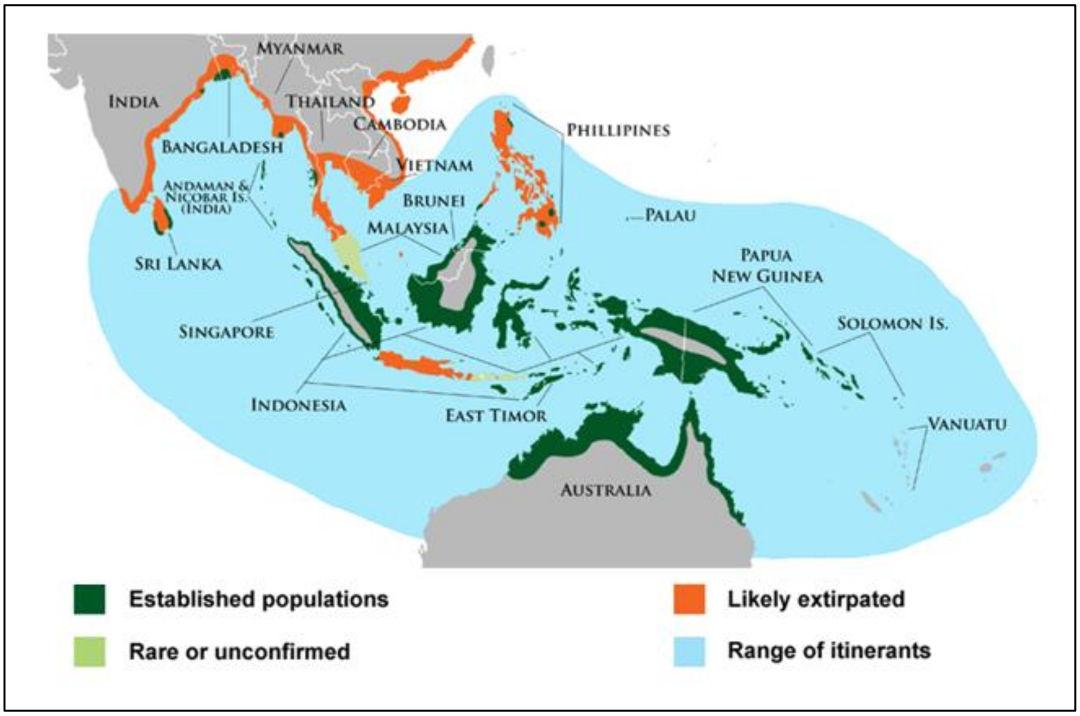


Figure 1.2. Global distribution of the estuarine crocodile (Britton, 1995)

Estuarine crocodiles are semi-aquatic, oviparous reptiles that spend more time in the water than on land (Campbell *et al.,* 2010; Read *et al*., 2004). Despite its most common name (saltwater crocodile), suggesting a marine-based habitat, the species thrives in non-tidal freshwater rivers, swamps, freshwater lakes, marshes, and mangrove forests (Lewis *et al*., 2013). In fact, some of the highest densities of estuarine crocodiles have been reported freshwater swamps that are heavily vegetated and away from tidal exposure (Webb *et al.*, 1977), which is also the primary area for breeding, nesting and recruitment (Cox, 1985).

In the marine environment, the estuarine crocodile inhabits tidal rivers and creeks. Movement between different habitats occurs between the dry and wet season, causing individuals to disperse, occupying offshore islands and coasts, and make journeys at sea in search of new rivers (Webb *et al*., 2018). As juveniles are raised in freshwater areas, these areas are dominated by dominant, territorial adults, whereas sub-adult individuals normally leave the area involuntarily due to social status and move into more fringed saline habitats. Among these individuals, the less dominant ones that fail to establish a territory are either killed or forced out into the sea where they move around to locate a new river. Recent data also suggest that large individuals move between countries for example between Australia-Timor Leste and Malaysia-Singapore (Webb *et al.*, 2021).

Estuarine crocodiles exhibit high site fidelity in spite of their ability to travel long distances, with long-distance travels linked to translocation. Breeding sites and seasonal feeding sites (e.g. sea turtle nesting grounds) are also huge factors for long distance travels among large individuals (Webb *et al*., 2021). The species has an ontogenetic shift in diet, that is a change in diet as they increase in size from juveniles to adults. Juvenile estuarine crocodiles primarily consume small prey items such as insects, crustaceans, frogs, and small fish, which are abundant in their freshwater habitats. As they mature, their dietary preferences expand to include larger prey. Adult estuarine crocodiles are opportunistic apex predators capable of taking down a wide variety of prey, including birds, mammals, and larger fish. They are known to hunt species like wild pigs, deer, water buffalo, and even sharks in coastal waters (Britton, 2012). Their diet reflects the ecological niches they occupy, from freshwater rivers and swamps to estuaries and coastal marine environments.

Estuarine crocodiles exhibit sophisticated predation patterns that capitalize on their powerful physical attributes and stealthy behaviour. They are ambush predators, relying on their camouflaged bodies and patient hunting strategies to capture unsuspecting prey. Crocodiles often lie in wait near the water's edge, submerging most of their bodies while keeping their eyes and nostrils above the surface. This stealth approach allows them to surprise prey with sudden, explosive attacks. Their powerful jaws and sharp teeth enable them to deliver a lethal bite, exerting one of the strongest bite forces recorded in the animal kingdom, which helps them secure and tear apart large prey (Erickson *et al*., 2012). Additionally, estuarine crocodiles exhibit remarkable swimming abilities, allowing them to pursue prey over considerable distances. These predation patterns and dietary habits underscore the estuarine crocodile's role as a top predator in its ecosystem, maintaining the balance of species populations within its habitat. Their eating habits help maintain the structure and function of the ecosystem and are thus considered as “keystone species” (Ross, 1998).

Due to their high adaptability to water salinity, the survivorship of estuarine crocodiles is high in natural populations (Grigg & Kirshner, 2015). This has allowed for the species to exist in a very large geographic range (Ross, 1998). They are long-lived and have extensive reproductive lifespans. It takes several years for adults to reach sexual maturity, where males reach at least 3.5 meters in length and females at least 2.5 meters (Webb & Manolis, 1989). However, despite laying a large clutch of eggs, many of the eggs do not hatch. On top of this, the hatchlings that do make it past the egg stage have very high mortality rates (49%) mainly due to predation (Brien *et al.*, 2014). In degraded habitats, or areas with very small or depleted crocodile populations, hatchling mortality rates are much less (15.5%) owing to the reduced rates of predations by other adult individuals (Webb *et al.*, 1977).

Estuarine crocodiles exhibit specific nesting habits that are closely tied to their reproductive success and the survival of their offspring. Female estuarine crocodiles typically select nesting sites in secluded and undisturbed areas near water bodies, such as riverbanks, mangrove swamps, and coastal regions. These sites provide the necessary moisture and temperature conditions for egg incubation. The females construct mound nests using vegetation, mud, and sand, which can measure up to one meter in height and two meters in diameter (Webb & Manolis, 1989). The choice of nesting materials and site location is crucial, as it helps regulate the nest temperature and protect the eggs from potential predators and environmental fluctuations.

The nesting season for estuarine crocodiles varies geographically but generally aligns with the wet season, which provides the necessary humidity for successful egg incubation. In Northern Australia, nesting typically occurs between November and March, coinciding with the monsoon rains, while in Southeast Asia, the timing can vary between regions (Britton, 2012). Female crocodiles lay between 40 and 60 eggs per clutch, and the incubation period lasts approximately 90 days, although this can fluctuate based on environmental factors such as temperature and moisture (Richardson *et al.*, 2002). Throughout the incubation period, the female remains close to the nest to guard it from predators and other threats, demonstrating a high level of parental investment (Campbell *et al.*, 2010). Once the eggs are ready to hatch, the female assists by uncovering the nest and, in some cases, gently transports the hatchlings to the water in her mouth, significantly increasing their chances of survival (Fukuda & Cuff, 2013). Understanding these nesting behaviors and habitats is crucial for conservation efforts, as protecting these sites from human disturbance and environmental degradation is essential for the species' long-term survival (Webb & Manolis, 1989).

Estuarine crocodiles face a multitude of threats that jeopardize their survival across their vast range. Habitat destruction is a primary concern, driven by rapid urbanization, agricultural expansion, and deforestation. Wetlands, mangroves, and estuaries - critical habitats for these crocodiles - are being degraded at an alarming rate. In Southeast Asia, particularly in countries like Indonesia and Malaysia, extensive logging and conversion of mangroves into palm oil plantations have drastically reduced available habitats for estuarine crocodiles (Giri *et al*., 2011). Such habitat loss not only diminishes the space available for crocodiles to live and breed but also impacts the abundance of prey species, further stressing crocodile populations (Fukuda *et al*., 2013). The loss of these vital ecosystems is compounded by pollution, overfishing, and increased human-crocodile conflicts, all of which place further pressure on these ancient reptiles (Ross, 1998).

Another significant threat to estuarine crocodiles is illegal hunting and poaching, primarily for their valuable skins and, to a lesser extent, for their meat. Despite international protections under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), illegal trade persists. Crocodile skins are highly prized in the fashion industry, leading to continued poaching in countries where enforcement of wildlife protection laws is weak (Webb *et al*., 2010). This illegal activity not only directly reduces crocodile numbers but also disrupts social structures and breeding patterns, which can have long-term impacts on population viability.

Human-crocodile conflict is another pressing issue, particularly in regions where human populations are expanding into traditional crocodile habitats. As people and crocodiles increasingly come into contact, the risk of attacks on humans and livestock rises, often leading to retaliatory killings of crocodiles. In places like Northern Australia, India, and parts of Southeast Asia, such conflicts are a significant cause of mortality for estuarine crocodiles (Whitaker & Whitaker, 2008; Somaweera *et al*., 2013; Fukuda *et al*., 2014). Managing these conflicts requires comprehensive strategies that include community education, habitat management, and the development of rapid response teams to handle conflict situations, all aimed at reducing the likelihood of encounters and promoting coexistence (Caldicott *et al.*, 2005).

Pollution and climate change also pose emerging threats to estuarine crocodiles. Pollutants such as heavy metals, pesticides, and plastics accumulate in aquatic ecosystems, impacting the health of crocodile populations through bioaccumulation and contamination of their prey (Rainwater *et al*., 2002; Taylor *et al*., 2017). Climate change, with its associated rise in sea levels, changes in salinity, and increased frequency of extreme weather events, further threatens the habitats and reproductive success of estuarine crocodiles. For instance, rising sea levels can inundate nesting sites, while temperature changes can affect the sex ratio of hatchlings, skewing populations towards one gender and potentially leading to future reproductive challenges (Mitchell *et al*., 2008). Addressing these multifaceted threats requires a holistic approach that combines conservation, policy intervention, and community engagement to ensure the long-term survival of estuarine crocodiles (Campbell *et al*., 2010).

The commercial trade of estuarine crocodile skins has a long and complex history, driven by the high demand for their hides, which are renowned for their quality, durability, and luxurious appeal. Estuarine crocodile leather is one of the most sought-after materials in the fashion industry, used in high-end products such as handbags, belts, shoes, and wallets (Thorbjarnarson, 1999). This immense demand led to widespread hunting and poaching, especially during the mid-20th century, which drastically reduced wild crocodile populations (Webb *et al.*, 2010). As populations became critically endangered, international regulations were introduced to control the trade. One key measure was the listing of *C. porosus* under Appendix I and 11 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which restricted commercial trade to protect the species from extinction (CITES, 2021). These measures have been instrumental in stabilizing and recovering wild crocodile populations in various regions.

Despite international regulations, the illegal trade in crocodile skins continues, driven by the high prices these products can fetch on the black market and the challenges of enforcing wildlife protection laws in some regions (Thorbjarnarson *et al.*, 2006). Poaching remains a significant threat to crocodile populations, especially in areas with weak law enforcement and where economic incentives for illegal hunting are strong. For example, in parts of Southeast Asia, crocodiles are still being illegally hunted, and their skins are smuggled across borders to meet the high international demand (Fukuda *et al.,* 2019). This illegal trade undermines conservation efforts and presents serious challenges to the sustainable management of crocodile populations. Conservation organizations and enforcement agencies are working to curb these activities through increased surveillance, stricter penalties, and international collaboration (Webb *et al*., 2010).

To mitigate the conservation issues associated with the commercial trade, many countries have implemented regulated crocodile farming and ranching programs aimed at satisfying the demand for crocodile leather without depleting wild populations (Fukuda *et al.,* 2019). Australia, for instance, has developed a successful crocodile farming industry that produces high-quality leather while ensuring that wild crocodile populations are sustainably managed and protected (Fukuda *et al.,* 2013). These farming operations are closely monitored to comply with CITES regulations, ensuring that the trade remains legal and traceable (CITES, 2021). Additionally, some farming programs contribute to conservation efforts by releasing captive-bred crocodiles back into the wild, supporting the recovery of wild populations (Webb *et al.,* 2010). This balance between commercial exploitation and conservation is essential for the long-term sustainability of *C. porosus* populations and the ecosystems they inhabit.

1.3 Population Demographics

The human population size is increasing by the day. In parallel, dramatic decrease in populations of a variety of flora and fauna, including wildlife populations have been occurring. As such, there is an urgent need to monitor and understand the impact of anthropogenic resources on wildlife populations (Sala *et al*., 2000). Over the years, many tools have been developed to measure wildlife population change (Norris, 2004). However, relying solely on population trend data can lead to ambiguous conclusions being drawn (Schaub *et al*., 2010). Fundamentally, to understand the environmental causes of change, particularly in vertebrate species, knowledge of the demographic processes underlying those changes is needed (Caswell, 2001).

Population dynamics encompasses changes in abundance, as well as the factors that contribute to those changes (Gotelli, 2001). This includes an assessment of population status and population vitality. Population status covers the current state of abundance, sex ratio and age of a population whereas population vitality covers the demographic health and self-sustaining ability of a population which include reproductive rates. Constructing models and management plans dealing with aspects such as endangered species and harvest depend principally on approximation of abundance and growth rates (Mills, 2007).

A meticulous monitoring program is an important tool for assuring the successful conservation, management and sustainable use of biodiversity in its distinct levels (Mancina & Cruz-Flores, 2017). At the population level, monitoring allows for evaluation of changes in demographic parameters and permits inspection of associations of these parameters with temporal and spatial variation in environmental factors (Tucker *et al,* 2005). As such, monitoring is an essential element in the formation of sustainable and viable policies (Chediack, 2009).

Demographic studies often involve long-term monitoring programs that track individual animals across their lifespan, providing data on survival probabilities and reproductive output. For instance, research on avian populations has elucidated the impacts of climate variability on nesting success and juvenile survival rates, highlighting the importance of demographic data in predicting species' responses to environmental fluctuations (Norris & Marra, 2007). Such studies also contribute to conservation efforts by identifying critical life stages and habitats essential for population persistence, guiding management strategies aimed at enhancing habitat quality and minimizing threats.

Besides that, demographic analyses play a crucial role in wildlife management and conservation planning by informing sustainable harvest quotas, reintroduction programs, and habitat restoration initiatives (Gaillard *et al.*, 2010). By assessing population structure and demographic trends, managers can implement adaptive management strategies that maintain viable populations while ensuring ecosystem integrity. This interdisciplinary approach underscores the importance of demographic studies in addressing conservation challenges and safeguarding the biodiversity and ecological functions of wildlife populations worldwide.

To specify crocodilian populations, careful monitoring is emphasized not only due to the functional role crocodilians play in their ecosystems, but also because of the ongoing human-crocodile conflict. In areas where human and crocodile territories overlap, the consequences can be severe for both parties. A holistic management strategy that includes mapping crocodile occupancy, distribution, and densities can help mitigate these conflicts (Fukuda *et al.*, 2014). Often, lethal control is employed as a solution to conflicts with crocodilians. However, to justify such measures, it is essential to thoroughly understand the problem species and the dynamics of its population. Population models are necessary to track the immediate effects that lethal control has on local, regional, and even continental populations, while also predicting how these populations will respond over time (Webb & Manolis, 1989).

Monitoring programs in several countries with significant crocodilian populations have been implemented to ensure sustainable use of crocodiles for their skin, meat, and ecotourism potential, making them economically important resources (Webb *et al*., 2010; Barrios-Quiroz & Cremieux, 2018). For instance, in Australia, such programs have been key in both conservation and commercial utilization, helping manage *C. porosus* populations while supporting sustainable crocodile farming and tourism (Fukuda *et al.,* 2007). These integrated approaches help balance the need for wildlife conservation with the commercial benefits of crocodile management.

Growth patterns differ substantially in vertebrates. A monophasic pattern is typically observed in mammals and other endothermic vertebrates whereby growth rates decrease as body sizes increase (Passos *et al*., 2014). On the other hand, a polyphasic growth is seen in ectothermic vertebrates such as crocodilians, where growth rates are linked to environmental variables such as water temperature and levels which can affect their ability to find and digest food, ultimately affecting their growth (Pina and Larriera, 2001). This has been reported for several crocodilian species such as *C. porosus, C. johnsoni, C. niloticus* and *Caiman crocodilus* (Magnusson & Sanaiotti, 1995).

The most widely used approaches for estimating population parameters for crocodilian populations are nocturnal counts based on eye-shine detection and capture-mark-recapture analysis (Garcia-Grajales *et al*., 2007). However, both approaches experience biases linked with flawed detection and spatial variation in the environment. This limits their capacities to differentiate temporal or random changes in population dynamics (Llobet & Seijas, 2003). However, in recent years, statistically formalized hierarchical models have been used widely as methods to model detection probabilities, relating it to density estimates, and to spatial and temporal variables in the environment (Kerry & Royle, 2015). Such models have been employed in many crocodilian population studies (Mazzoti *et al*., 2019).

Demography studies in crocodiles are fundamental for unravelling the intricate dynamics of their populations, encompassing crucial aspects such as survival rates, reproductive strategies, and age structure. These studies integrate field observations with statistical analyses to assess population trends and understand the factors influencing crocodile demographics in their natural habitats. By quantifying parameters such as growth rates, age at maturity, and longevity, researchers gain insights into the resilience of crocodilian populations to environmental changes and human impacts (Brien *et al*., 2018).

Crocodile demography studies often involve long-term monitoring efforts that track individual animals across different life stages. For instance, research on the Nile crocodile has provided valuable data on survival rates from hatchling to adult stages, elucidating the factors affecting juvenile mortality and the recruitment of individuals into the breeding population (Stevenson *et al.,* 2020). Such studies are essential for informing conservation strategies aimed at maintaining sustainable populations and mitigating threats such as habitat loss and poaching.

Demographic analyses play a critical role in understanding the reproductive ecology of crocodiles, including nesting behaviours, clutch sizes, and incubation periods. Studies on species like the saltwater crocodile have revealed adaptations in reproductive strategies to different environmental conditions, highlighting variations in nesting site selection and maternal care behaviours (Campbell *et al.,* 2013). These insights are crucial for identifying key breeding habitats and implementing measures to protect nesting sites from human disturbance and predation, ensuring the reproductive success and genetic diversity of crocodilian populations.

In addition to their ecological significance, crocodile demography studies contribute to the management and conservation of these iconic species. By assessing population structure and demographic trends, conservationists can develop effective management plans that balance sustainable use with biodiversity conservation goals (Milián-García *et al.*, 2020). This holistic approach underscores the importance of integrating demography studies into broader conservation strategies aimed at safeguarding crocodilian populations and their habitats worldwide.

1.4 Spatial Dynamics in Ecology

Spatial ecology is a dynamic field within ecology that investigates how organisms interact with their environment across spatial scales, integrating ecological principles with spatial analysis techniques. It explores the distribution, movement patterns, and habitat utilization of wildlife populations, shedding light on the influence of environmental factors such as habitat structure, resource availability, and landscape configuration (Cushman & Huettmann, 2010). By clarifying these relationships, spatial ecology provides vital insights into ecological processes and conservation challenges, guiding management strategies aimed at preserving biodiversity and ecosystem function (Heller & Zavaleta, 2009). Advanced spatial technologies including geographic information systems (GIS), remote sensing, and GPS tracking are essential in capturing and analysing spatial data, enabling researchers to predict species distributions, delineate critical habitat areas, and assess population connectivity (Kays *et al.*, 2015). Overall, spatial ecology contributes significantly to understanding the impacts of anthropogenic activities on wildlife and ecosystems, informing sustainable conservation practices and landscape management decisions.

Spatially explicit models in ecology provide predictive power for conservation planning and management. These models incorporate spatial data on habitat quality, connectivity, and human disturbances to identify areas of high conservation value and prioritize conservation actions (Levin *et al.*, 2013). For example, in avian ecology, spatial models play a crucial role in understanding the migratory connectivity and habitat use of birds, particularly during their migration and non-breeding periods. These models helped visualize and predict the effects of spatial connections, such as migration routes and stopover sites, on species' populations. By mapping these spatial patterns, researchers were able to assess how habitat loss and climate change impacted the population dynamics of land birds (McKinnon *et al.*, 2013). The use of geolocators provided precise data on these migratory routes, offering insights into how habitat changes in both breeding and wintering sites affected the viability of migratory bird populations. Such approaches not only enhance our understanding of wildlife ecology but also inform policy decisions aimed at mitigating human-wildlife conflicts and preserving biodiversity in a rapidly changing world.

Additionally, spatial technologies, such as remote sensing and geographic information systems (GIS), have revolutionized our ability to study wildlife at varying spatial scales. These technologies enable researchers to monitor individual movements in real-time, map habitat use patterns, and quantify spatial relationships between species and their habitats (Kays *et al.*, 2015). By integrating these spatial datasets with ecological models - mathematical or computational frameworks that simulate species-environment interactions - scientists can address complex questions related to species conservation, ecosystem management, and the resilience of wildlife populations in the face of environmental challenges.

Crocodilian spatial ecology delves into the intricate interactions between crocodilians and their environments across varying landscapes and habitats. This field integrates ecological principles with spatial analysis techniques to unravel how environmental factors shape the distribution, movement patterns, and habitat preferences of crocodilian species. Understanding these dynamics is crucial for effective conservation and management strategies, particularly in regions where crocodilians play significant ecological roles as apex predators and keystone species (Ross *et al.*, 2020).

Crocodilians exhibit complex behaviours influenced by their ecological requirements and environmental conditions. For instance, studies on the American alligator have highlighted their reliance on specific habitat types such as freshwater marshes and brackish estuaries, where water levels and temperature gradients play critical roles in their daily activities and reproductive success (Mazzotti *et al.*, 2019). Spatial ecology approaches, including GIS mapping and satellite telemetry, have been instrumental in tracking crocodilian movements, delineating home ranges, and identifying core habitats essential for their survival (Brien *et al.*, 2018).

Moreover, crocodilian spatial ecology contributes to broader conservation efforts by assessing the impacts of habitat fragmentation, climate change, and human activities on population dynamics and genetic connectivity. By mapping habitat suitability and analysing landscape features that facilitate or hinder crocodilian movements, researchers can prioritize conservation areas and implement habitat management practices that enhance ecosystem resilience and support sustainable crocodilian populations (Milián-García *et al.*, 2020). This interdisciplinary approach not only advances our scientific understanding of crocodilian ecology but also informs adaptive management strategies crucial for their long-term conservation in a changing world.

Spatial ecology studies also play a crucial role in mitigating human-crocodile conflicts by providing valuable insights into the spatial behaviour and habitat preferences of crocodilians. By mapping crocodile movements and identifying high-conflict areas where human activities intersect with crocodile habitats, researchers can recommend targeted management strategies to minimize interactions and reduce risks to both human populations and crocodiles (Dinets *et al.*, 2013). For instance, spatial analyses have helped identify corridors of crocodile movement across landscapes, allowing authorities to implement protective measures such as fencing, signage, and controlled access to water bodies in areas prone to conflict (Campbell *et al.*, 2015).

Understanding crocodile spatial ecology aids in predicting and mitigating potential conflict scenarios through proactive management practices. By delineating crocodile home ranges and key habitat areas, conservationists can establish buffer zones and implement habitat modifications that steer crocodiles away from densely populated human areas while promoting coexistence in shared landscapes (Hockings *et al.*, 2015). Spatial data on crocodile behaviour also inform public awareness campaigns and educational programs aimed at enhancing community understanding of crocodile ecology and safe practices for living alongside these apex predators. Ultimately, integrating spatial ecology studies into human-crocodile conflict management strategies enhances safety measures for both humans and crocodiles while fostering sustainable conservation practices.

1.5 Population Genetics

The field of population genetics is nearly 100 years old, and during that time it has developed a rich body of mathematical models to describe how allele frequencies change over time. Traditional population genetic methods focused on the characterization of genetic variation comparing observed patterns of expected patterns of variation following principles like the Hardy-Weinberg Equilibrium or linkage equilibrium models. The application of principles of allele frequency change following genetic drift under the Wright-Fisher model empowered population geneticist to propose models to explain how populations evolve over time. However, an import development in the last 50 years was the development of the coalescent theory, which enables modeling gene genealogies back in time (the opposite of the Wright-Fisher model) to determine which processes explain the way gene genealogies look like. The combination of the development of molecular genetics and of improved computational resources, have enabled population genetics to efficiently apply the theoretical models of the coalescent to characterize in detail the history of natural populations and describe how these have responded to range of environmental pressures driven by the ever-increasing human population and its associated landscape changes.

Today, technological expansion has aided in the development of straightforward and inexpensive methods that can be adopted in wildlife research (Oyler-McCane & Leberg, 2015). Wildlife populations often face challenges with quite a few anthropogenic factors such as habitat fragmentation, pollution, climate change, invasive species, harvesting, illegal hunting etc. which usually results in the inability of a wild population to sustain, ultimately causing extinction. While all these factors have been the focus and utmost importance for wildlife conservation, the evolutionary consequences (genetic drifts) of these occurrences are overlooked (Bhaskar & Sharon, 2022). Genomics and genetic studies address this and make available critical information that is needed to form management plans (Hohenlohe *et al*., 2021).

The uprise of genomics has changed the field of population genetics by permitting high-quantity sequencing to be applied in any organism, including natural populations that are rare and hard to study (Rajora, 2019). As a result, genetic methods have become a significant instrument for understanding wildlife biology such as disease and population dynamics. Consequently, this allows for direct and effective conservation and management actions to be implemented on wildlife population and their habitats (Hohenlohe *et al.*, 2021).

The foundation of conservation genetics lies strongly on the theory that inbreeding, resulting from mating between closely related individuals, and low levels of genetic diversity, is the main cause for reduced fitness and adaptability in natural populations. This is more apparent in small populations where the likelihood of breeding between close relatives is high and the effects of genetic drift is more obvious (O'Brien, 1994). Identifying the exact genetic processes that cause a decline in natural populations, however, is difficult. It is almost impossible to identify the specific relationship between heterozygosity, allelic variation and fitness at a given time, making reliable predictions hard to make. Moreover, the concept of fitness is inherently fluid, as its estimation in natural settings typically requires tracking reproduction across generations. This process has become more feasible in recent years with the development of hypervariable DNA markers, which allow for the identification and tracking of lineages (Sarre & Georges, 2009). By estimating allele frequencies in two different generations, we can use this information to quantify fitness as a numerical value, reflecting the contribution of specific alleles to reproductive success.

The field of ecology generally limits itself to the here and now, with the assumption that the course of evolution is too slow and is insignificant in an ecological timeframe. It does not emphasize on the interconnection between the two fields (Sarre & Georges, 2009). However, today many molecular ecology experimental studies on population data provide robust evidence that low levels of genetic variation bring about extinction, and this correlation is not just confined to small populations (Spoelman *et al*, 2004; Reed *et al*., 2007).

The ability to assess the genetic divergence among individuals, populations, and species has revolutionized evolutionary biology. This is largely due to advances in molecular markers, which serve as tools for generating genetic data, and the field of population genetics, which interprets these data to study evolutionary processes. Today, the techniques available in genetics allow for the examination of different sections of a genome which provide different vital information. Complete sequencing of homologous DNA fragments from various organisms using polymerase chain reaction (PCR) is the most robust and direct technique to obtain information on genetic variation and the degree of divergence (Harrison, 1989).

The two most common genomes used in genetic research of animals are the nuclear genome and the mitochondrial genome. The nuclear genome is located in the cell nucleus and exhibits biparental inheritance, where offspring inherit one allele from both the paternal and maternal sides for each gene. In contrast, the mitochondrial genome, located in the mitochondrion, is primarily maternally inherited, although rare cases of paternal leakage, where mitochondria from the father are inherited, have been observed (White *et al.*, 2008). The mitochondrial genome is well mapped in many species, in contrast to the more complex nuclear genome. The evolutionary process of the nuclear DNA is slow, though certain regions such as microsatellites evolve rather quickly. Comparatively, the mitochondrial DNA evolves quickly and areas such as the control region evolve very rapidly, making the mitochondrial DNA and some regions of the nuclear DNA ideal targets for population genetic studies (Avise, 1994). Mitochondrial DNA displays substantial amount of variation among individuals both within and among populations and has demonstrated to be an effective marker for the study of population structure (Avise *et al*. 1987; Avise, 2000).

Crocodilians have evolved at a relatively slow pace over millions of years, with this gradual change reflected in their karyotypes, where chromosome numbers and structures have remained stable. In contrast to other vertebrates that have undergone significant evolutionary changes, extant crocodilian species have preserved many ecological and morphological features. The relatively small number of crocodilian species worldwide, despite their widespread distribution, is likely influenced more by ecological factors and geographical isolation than by mutation rates alone. While mutation rates in crocodilians are slower compared to most vertebrates, the accumulation of genetic variation over millions of years, shaped by natural selection and geographic barriers, has enabled these species to adapt and survive (Grigg *et al.*, 2001; Green *et al.*, 2014).

Understanding the genetic structure and connectivity of crocodilian populations across landscapes is crucial for effective conservation and management strategies. Landscape genetics integrates principles from landscape ecology with population genetics, providing insights into how landscape features influence gene flow, genetic diversity, and population dynamics (Manlik *et al.*, 2020). In the context of crocodiles, this approach explores how rivers, wetlands, and terrestrial habitats act as corridors or barriers to gene flow, shaping population differentiation and genetic diversity (Brien *et al.*, 2018). For instance, studies on the American alligator have revealed significant genetic structuring across riverine systems, indicating the role of water bodies in restricting gene flow and promoting local adaptation (De Jesús-Crespo *et al.*, 2019). By elucidating these landscape-genetic relationships, researchers can prioritize conservation efforts in key areas that maintain genetic connectivity and ecological resilience.

Moreover, landscape genetics facilitates the identification of evolutionary processes driving genetic divergence among crocodilian populations. Natural and anthropogenic factors such as habitat fragmentation, urbanization, and climate change influence how landscapes shape genetic patterns over time (Somaweera *et al.*, 2018). Genetic studies can delineate distinct management units and identify priority conservation areas based on genetic uniqueness and evolutionary potential (Milián-García *et al.*, 2020). By integrating landscape genetics into conservation planning, managers can develop strategies that enhance habitat connectivity and mitigate the impacts of landscape changes on crocodilian populations, ensuring their long-term survival in dynamic environments.

1.6 Conservation Management: A Regional Overview

Regional focus in conservation management refers to the tailored strategies applied within specific geographical areas to address the unique environmental challenges and biodiversity concerns of that region. Each region possesses distinct ecological characteristics, species compositions, and environmental threats, which require targeted conservation efforts. These factors include habitat types, climate conditions, levels of human activity, and species interactions, all of which play a critical role in shaping effective management practices (Margules & Pressey, 2000). By considering these factors at a regional level, conservation strategies can be more accurately designed to preserve biodiversity and maintain ecosystem function, ensuring that local environmental needs are met.

The interconnectedness of regional focus and conservation management lies in the necessity for site-specific solutions that cater to the unique challenges of an area. Conservation management cannot be applied uniformly across different regions because ecosystems vary widely in terms of species richness, threats, and human influences (Grumbine, 1994). For example, conservation strategies for protecting tropical rainforests in Southeast Asia differ significantly from those required for savannah ecosystems in Africa, due to the different species and ecological processes involved. Regional focus allows for the inclusion of local knowledge and practices, which often prove valuable for long-term conservation success, while also incorporating scientific insights on biodiversity and ecosystem health (Balmford *et al.*, 2001).

Moreover, regional conservation efforts contribute to global biodiversity conservation by focusing on the preservation of locally significant species and habitats, which collectively maintain global ecological balance. Effective regional management strategies enhance genetic diversity and promote the resilience of species to environmental changes, including habitat fragmentation and climate change (Gaston & Fuller, 2008). Regional initiatives, when implemented in harmony with broader global conservation goals, ensure that conservation actions are contextually appropriate and sustainable, supporting both local ecosystems and the larger global environmental agenda.

One of the key tools in regional conservation management is Population Viability Analysis (PVA), which is used to assess the long-term viability of species populations. PVA models simulate the future dynamics of a population based on demographic, genetic, and environmental data. These models help conservationists understand the likelihood that a population will persist over time under different scenarios, such as varying levels of habitat destruction, climate change, or human-induced mortality. By integrating PVA into regional management strategies, conservationists can make data-driven decisions about which conservation actions will be most effective in ensuring species survival (Brook *et al.*, 2000). For example, PVA can be used to predict how habitat fragmentation may affect the connectivity of crocodile populations, or how changes in breeding success could influence population growth. This approach is particularly valuable in areas where limited resources require prioritizing certain management actions, as it allows for the testing of various strategies before they are implemented (Lande, 1993). PVA provides a framework for adaptive management, where strategies can be adjusted based on continuous monitoring of population health and environmental changes.

When applying a regional focus to crocodile conservation, it becomes evident that these species face distinct challenges based on their specific habitats and regions. Crocodiles, such as the estuarine crocodile, are found in a variety of ecosystems, from riverine systems to coastal mangroves, each of which poses unique conservation challenges. Effective regional management is crucial for maintaining the balance between human activities and crocodile populations, as habitat loss, human-crocodile conflicts, and illegal hunting continue to threaten their survival in many areas (Webb *et al*., 2010). By tailoring conservation strategies to specific regional threats and ecological characteristics, management practices can ensure that crocodile populations remain healthy and play their vital ecological roles as apex predators. Moreover, these region-specific efforts contribute to broader global conservation goals by preserving biodiversity and promoting the resilience of crocodile populations to environmental changes, thereby ensuring the long-term sustainability of these species (Fukuda *et al*., 2019).

Local communities in Sabah, Malaysia, navigate a complex relationship with the rivers that are shared territories with diverse wildlife, including crocodiles. These rivers are essential lifelines for communities, providing water for drinking, irrigation, and fishing resources crucial for sustenance (Stuebing *et al*., 2014; Brien *et al*., 2018). However, this close dependence on riverine ecosystems necessitates coexistence with wildlife, posing challenges and opportunities for community well-being and wildlife conservation alike.

The interaction between local communities and wildlife in Sabah's rivers is shaped by traditional knowledge and practices aimed at minimizing conflicts and maximizing coexistence. For instance, communities often employ strategies such as avoiding specific areas or adjusting fishing practices to reduce encounters with crocodiles and other wildlife (Messel *et al*., 1995; Stuebing *et al*., 2014). These practices reflect the adaptive strategies developed over generations to navigate shared habitats with wildlife while ensuring safety and livelihood sustainability.

Moreover, community-based conservation initiatives are instrumental in fostering harmonious relationships between humans and wildlife in Sabah. These initiatives empower local communities to participate actively in conservation efforts, promoting sustainable resource management and habitat protection (Shine *et al.*, 2019). By integrating local knowledge with scientific insights, these initiatives not only enhance wildlife conservation but also strengthen community resilience and well-being in the face of environmental challenges. Through collaborative efforts, Sabah's communities and wildlife continue to coexist in a balanced ecosystem that supports both human livelihoods and biodiversity conservation goals (Fukuda *et al.*, 2019).

Crocodiles, particularly the estuarine crocodile, play a vital ecological role in Sabah, where they are apex predators crucial for maintaining the health of wetland ecosystems. These habitats, including coastal mangroves, riverine systems, and estuaries, provide essential breeding, nesting, and foraging grounds for crocodiles, highlighting their ecological significance (Stuebing *et al.*, 2014; Brien *et al.*, 2018). However, alongside their ecological importance, crocodiles in Sabah also present challenges due to human-crocodile conflicts arising from overlapping habitats and livelihood activities. Effective conservation management strategies are essential to mitigate these conflicts while ensuring the persistence of crocodile populations (Webb *et al*., 2010).

As of the latest assessments, the estuarine crocodile in Sabah is categorized by the International Union for Conservation of Nature (IUCN) as being of Least Concern (LC). This classification indicates that the species is not currently considered at immediate risk of extinction, primarily due to its widespread distribution across Southeast Asia and Australia, including various habitats within Sabah (IUCN Red List, 2023). The population status of estuarine crocodiles in Sabah are relatively stable compared to other regions where crocodiles face more significant threats from habitat loss, poaching, and human-wildlife conflicts (Stuebing *et al*., 2014).

Efforts to monitor and conserve estuarine crocodiles in Sabah include population assessments, habitat surveys, and community engagement initiatives aimed at promoting coexistence between crocodiles and local communities. These conservation measures are crucial for maintaining healthy crocodile populations and preserving their ecological roles in Sabah's aquatic ecosystems. Despite their status as Least Concern, ongoing conservation efforts remain essential to mitigate potential threats and ensure the long-term sustainability of saltwater crocodiles in the region (Stuebing *et al.*, 2014).

While the population in Sabah is reported to be relatively stable, conservation efforts are grounded in robust scientific research and management practices aimed at understanding and protecting crocodile populations. Research initiatives encompass ecological studies, population monitoring, and habitat assessments to gather crucial data on crocodile behaviour, demographics, genetics and habitat requirements (Dinets *et al.*, 2013). Such research is vital for informing conservation strategies that balance the needs of crocodiles with those of human communities reliant on the same aquatic and coastal habitats for their livelihoods.

Human-crocodile conflicts in Sabah primarily stem from interactions that result in attacks on humans or livestock, leading to safety concerns and negative perceptions among local communities. These conflicts often escalate into retaliatory killings of crocodiles, posing threats to population sustainability (Stuebing & Voris, 2015). Effective management of these conflicts requires a multifaceted approach that includes community engagement, education, and the implementation of mitigation measures. Conservation efforts also focus on infrastructure improvements such as the installation of barriers and signage around crocodile habitats to minimize human encounters and enhance safety for both residents and crocodiles (Stuebing *et al.*, 2014).

Community engagement plays a crucial role in crocodile conservation management in Sabah, fostering partnerships among local communities, government agencies, and conservation organizations. Initiatives promoting sustainable livelihood practices, alternative income sources, and ecotourism opportunities aim to reduce human dependency on crocodile-inhabited areas and alleviate pressures on crocodile populations (Shine *et al.*, 2019). By involving stakeholders in conservation decision-making and fostering a shared responsibility for wildlife protection, the state of Sabah aims to achieve sustainable conservation outcomes while promoting harmonious coexistence between humans and crocodiles.

Moreover, the conservation management of crocodiles in Sabah involves policy frameworks and legal measures to regulate human activities in crocodile habitats effectively. Conservation policies seek to enforce habitat protection, species management plans, and guidelines for handling human-crocodile conflicts (Stuebing *et al.*, 2014). These measures are crucial for ensuring compliance with conservation goals and mitigating anthropogenic impacts on crocodile populations.

In conclusion, crocodile conservation management in Sabah faces the dual challenge of conserving biodiversity while addressing human-crocodile conflicts in a region experiencing rapid development. By integrating scientific research, community engagement, and adaptive management strategies, Sabah strives to protect its crocodile populations and safeguard the well-being of local communities. Continued collaboration and innovative approaches are essential for achieving sustainable crocodile conservation and fostering a balanced ecosystem in Sabah's diverse and ecologically rich landscapes.

1.7 Chapter overview

The main aim of this thesis is to enhance the understanding of the estuarine crocodile population in Sabah through a comprehensive examination of its ecology, genetics, and conservation status. This aim was achieved through addressing several key objectives, including the assessment of population demographics, spatial ecology, genetic diversity, and the evaluation of extinction risks. The current chapter (Chapter 1) lays out the background and motivation for the research carried out, providing the foundation for the subsequent chapters and their contribution to crocodile conservation in Sabah. The work to address the objectives of this study is presented in chapters dealing with the following topics:

Chapter 2 focuses on estimating the baseline population demographic information of the estuarine crocodile in Sabah. The primary objective was to collect key data on the population size, age distribution, and sex ratios using standard crocodilian census techniques. By addressing this question, the goal was to establish a foundational understanding of the current population status, which is critical for effective conservation management.

Chapter 3 investigates the spatial ecology of the estuarine crocodile population in Sabah. The aim was to track individual crocodiles using satellite technology to determine their movement patterns, home range, and habitat use. This research was designed to provide insights into the crocodiles' spatial behavior, identifying critical areas for conservation.

Chapter 4 explores the genetic diversity of the estuarine crocodile populations in Sabah. The objective was to assess the genetic health of the population by analyzing genetic markers to identify potential risks such as inbreeding or genetic bottlenecks. This study was crucial for understanding the long-term viability of the population and its ability to adapt to environmental changes.

Chapter 5 uses Population Viability Analysis (PVA) to assess the extinction vulnerabilities and predict future population trends of the estuarine crocodile in Sabah. The aim was to model the population's response to potential conservation scenarios, including harvesting and supplementation. This chapter also provides a comprehensive discussion of the outcomes from Chapters 2-4. This chapter synthesizes the results, addressing the main aim of the thesis and concludes by offering recommendations for future research and conservation efforts to ensure the long-term survival of crocodile populations.

CHAPTER 2

Demography and Population Structure of the Estuarine Crocodile in Sabah: Insights for Conservation Management

2.1 Introduction

A good understanding of an animal's population demography encompasses knowledge of population size, age structure, survival rates at different stages, reproduction rates and levels of immigration and emigration. When it comes to crocodilians in particular, Webb & Smith (1987) identified three levels of understanding population dynamics. Firstly, identifying whether a population is stable, decreasing or increasing, secondly, to determine the age structure of a population and to identify survival rates, reproductive rates as well as the extent of immigration and emigration, and lastly to obtain information on how a population responds to change or regulatory processes such as competition for resources and cannibalism. Effective techniques for monitoring and identifying these aspects in a population are fundamental in conservation efforts, especially when managing a threatened species such as the estuarine crocodile.

The estuarine crocodile is the largest and most widely distributed crocodilian with its distribution ranging from Southern India and Sri Lanka, across Southeast Asia, through the Philippines and Palau Islands, and down to Indonesia, Solomon Islands, Papua New Guinea and Northern Australia. Being a large predator that is potentially dangerous to humans (Webb & Manolis, 1989), the existence or growth of C. *porosus* populations in waterways such as freshwater and marine habitats is followed by an increase in the occurrence of 'problem crocodiles' that represent possible threat to humans (Walsh & Whitehead, 1993).

Despite their substantial distribution rage, C. *porosus* are listed in CITES appendix 1 except in Australia, Papua New Guinea and Indonesia due to habitat loss and over-exploitation (Than *et al.*, 2020). Since the early 1940s, the species was at risk of extinction across most of its range due to excessive wild harvest, illegal trade and commercial hunting for skin and meat. In Northern Australia and the Solomon Islands, C. *porosus* populations have gone through a massive recovery after protective measures were implemented in the 1970s and 1990s (Webb *et al.*, 2010; Fukuda *et al*., 2011). Due to this, the species is listed as Least Concern (LC) in the IUCN Red List (1996) despite having poor population statuses elsewhere and some statuses even unknown.

The conservation of C. *porosus* is a matter of contradiction for wildlife managers. While being known as 'problem crocodiles', estuarine crocodiles structure and balance the ecosystem through predation, nutrient cycling, and by shaping the vegetation community in the wetland environments they inhabit (Mazzotti *et al*., 2009). Despite being a source of tourist attraction in their natural habitat, any increase in the population abundance of *C. porosus* is known to reduce the amenity values that people seek to enjoy (Letnic & Connors, 2006). As such, the presence of C. *porosus* can significantly affect the use of freshwater rivers and riparian areas which also leads to an impact on the economic sector.

The estuarine crocodile lives in wetlands, coastal waterways, shorelines, mangrove-fringed tidal flats, tidal creeks etc. While they disperse inland through freshwater rivers, creeks and swamps (Semeniuk *et al*., 2011), mangroves also provide abundant food and protection for juvenile. There can be substantial discrepancy in the suitability of various microhabitats for crocodiles despite being in the same geographic region. In Australia for example, these microhabitats may comprise of mangrove fringed salt flats and tidal creeks, dense mangrove-inhabited delta, narrow mangrove-inhabited ravines, all of which have variable population abundance (Fukuda *et al*., 2007).

Beside this, environmental and anthropogenic factors such as vegetation structure, prey availability, human settlements and man-made structures influence the use of habitats by *C. porosus* (Mazzotti *et al*., 2019). Demographic studies done in Sri Lanka and Bangladesh revealed that salinity and proximity to human settlements had a significant impact on the population density of *C. porosus* (Aziz & Islam, 2018). Therefore, assessing natural habitat features as well as the presence of anthropogenic influence provide valuable insights into the regional distribution of *C. porosus*.

As a result of extirpation of much of its former range and current issues of habitat destruction, the *C. porosus* populations in Sabah are fragmented are thriving in only certain regions in the state. Although the crocodile populations appear to be stable in some rivers in Sabah, the apparent decline of crocodiles in other rivers is a cause of concern. Additionally, due to widespread unemployment (Lee, 2020), especially in rural areas, many rivers are used by villagers for swimming, fishing, traditional harvest of plants and animals and for other day-to-day activities. Such use of riverine environments has led to human-crocodile conflict generating a negativity perception about crocodiles in some areas. This has led to unregulated harvesting, killing of crocodiles, as well as disturbances of nesting areas. Given these circumstances, the status of the crocodile population in Sabah needs to be understood to create an integrated management plan which will hopefully address human-crocodile conflict especially for the local communities living adjacent to rivers.

The first constituent for a robust management plan should be a quantitative population survey to assess the population structure, distribution, and density. However, measuring the status of a crocodile population is intricate and is commonly subjected to several sources of uncertainty and bias (Games *et al*., 1992). Therefore, it is crucial that a detailed review on global crocodilian techniques should be undertaken in order to select the best possible survey strategy.

Several studies on the population dynamics of *C. porosus* have been conducted in Borneo (Cox & Gombek, 1985; Stuebing & Mohd Sah, 1992; Stuebing *et al*., 1994). However, currently there is inadequate data on the distribution and abundance of *C. porosus* in the state of Sabah. The first study on the population structure of *C. porosus* in Sabah was done by Whitaker (1984) over a six-week survey. In year 2002, a second survey was conducted by the Sabah Wildlife Department and the study revealed a ten-fold increase of crocodile numbers from the survey conducted in 1984. This chapter covers facets of a third survey conducted in Sabah that provides significant information on the current population status of the estuarine crocodile.

Primary Objective

To conduct a population survey of *C. porosus* in Sabah through spotlight surveys to characterize its current population status.

Secondary Objectives

1. To identify the abundance/density of *C. porosus* populations in Sabah.
2. To understand the distribution of *C. porosus* in Sabah.
3. To identify the population structure of *C. porosus* in Sabah.

Hypotheses:

1. The population of *C. porosus* in Sabah has increased from the last study conducted in 2002.
2. *C. porosus* is distributed throughout most biogeographical regions in Sabah.
3. There are more large-sized individuals of *C. porosus* living in waterways of Sabah compared to small-sized individuals.

2.2 Methodology

2.2.1 Sample Collection

A total of 30 spotlight surveys were conducted in 10 rivers in Sabah from April 2017 to October 2019. These 10 rivers were selected for analysis as they represent some of the largest river systems in Sabah (Figure 2.1). Additionally, several of these rivers are known hotspots for human-crocodile conflict making them priority areas for conservation and management efforts.

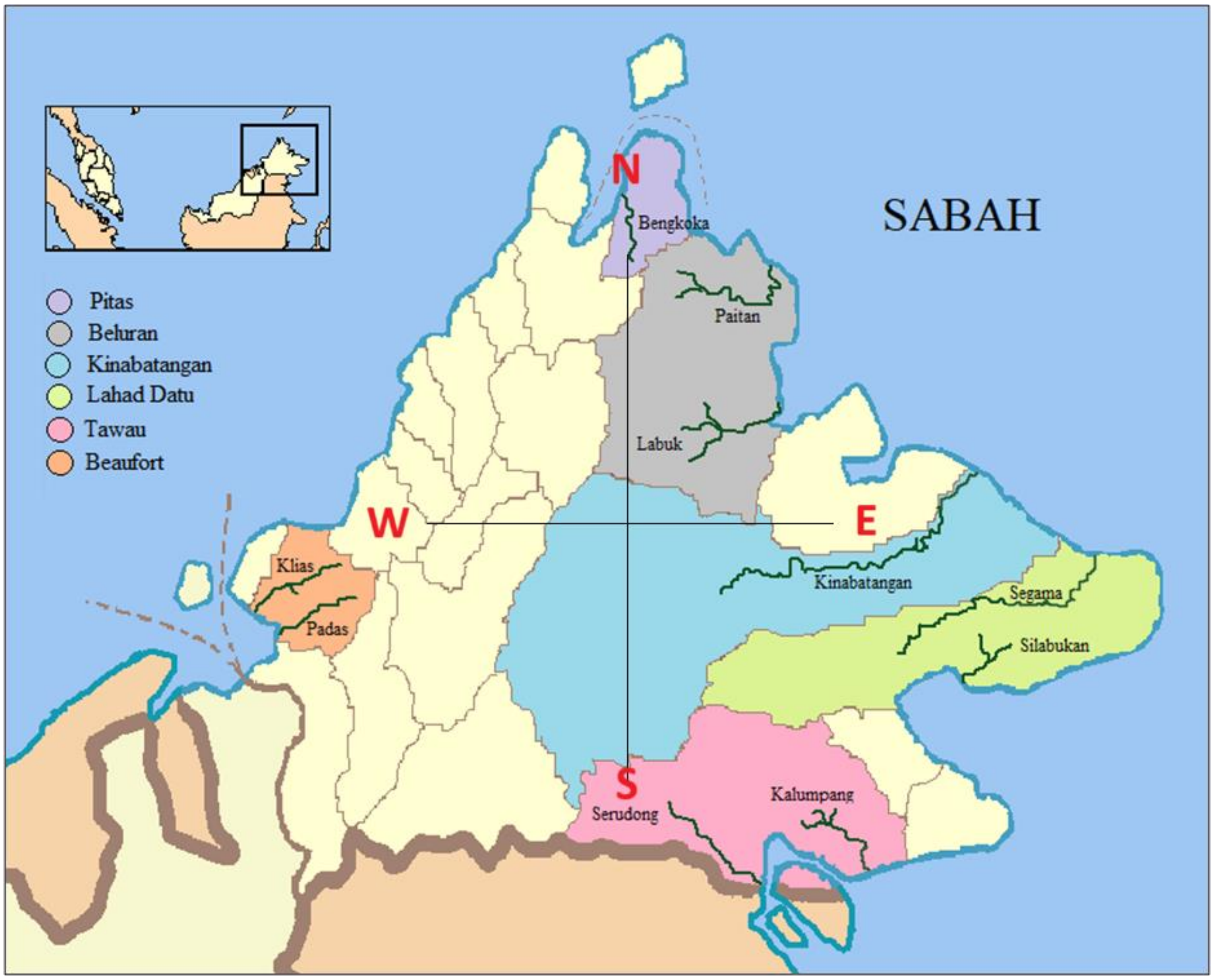


Figure 2.1. Map of Sabah showing the 10 sampling sights surveyed in this study. Rivers surveyed are shown in black with their name adjacent to the river. The districts of Sabah surveyed are show in colour; districts not studies are shown in light yellow.

Furthermore, previous surveys conducted in 1984 and 2002 included some of these rivers, allowing for valuable comparative analyses of population trends over time. Efforts were made to obtain a representative sample of Sabah's waterways and to ensure most biogeographical regions in Sabah were sampled. North, East, South and West coasts of Sabah were sampled comprising of six districts as shown

Visual encounters were carried out by two observers using a boat (myself and research assistant). Each stretch of river was surveyed upstream at night for approximately 50 km depending on the river. Surveys proceeded from downstream (the river mouth) to upstream (inland), with the survey boat staying ahead of the incoming tide (Figure 2.2). This maximizes the duration of water levels around low tide suitable for conducting surveys. The start and end points of each section were approximately the same between years, because crocodile abundance and distribution along a river varies over time and space (Fukuda *et al.*, 2007). In addition, the effect of seasonal changes in temperature and water level that affect crocodile behaviour (Webb, 1991) had to be minimized. Surveys were conducted during a low tide at night. Surveys within each biogeographical region were conducted at the same time each year to minimize variability in counts, ideally within the same two-week period. The exact date and time of a survey however depended on the river tide.

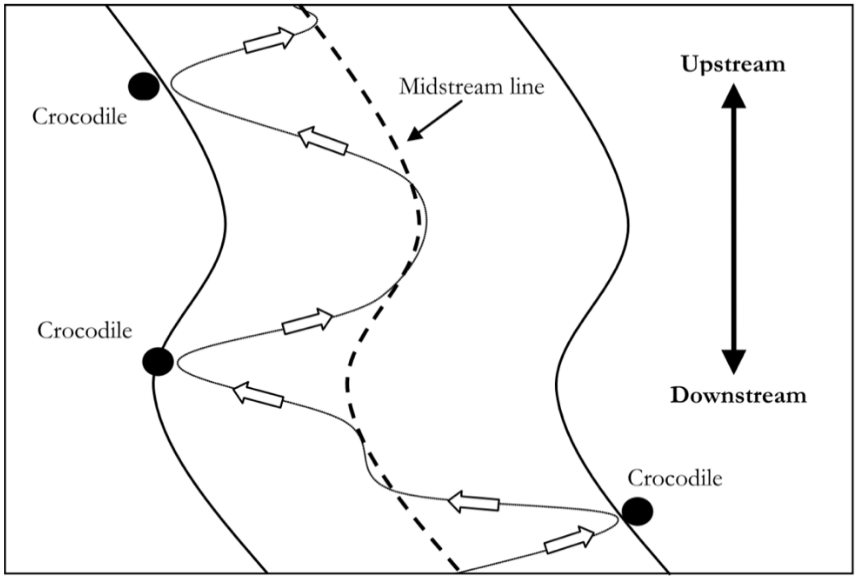


Figure 2.2. Spotlight survey method (Fukuda *et al.*, 2013)

The maximum survey time and distance covered (moving upstream) was largely determined by crocodile density and speed of survey. In tidal rivers with medium to high densities of crocodiles (>5 eye-shines detected per kilometre), average speed of progress along a river was between 10 and 12 km/h, allowing approximately 50 km to be surveyed in 6-8 hours. A H14.2 led Lenser head torch was used to identify the red eye shine of crocodiles. Once an individual was spotted, the boat was brought as close as possible to the animal. Once in close proximity to the animal, a GPS location, the habitat category and an estimated size of the animal were recorded.

Crocodile total length was assessed wherever possible and placed into a size category based on estimates made from the visible head length. The categories are detailed in Table 2.1. Any individual that was not able to be assessed for size was placed into the “eyes only” (EO) category.

Table 2.1. Classification used to estimate size of individuals during spotlight surveys.

Crocodile Class	***Individual Size (cm)***	***Category***
H	<60	Hatchling (H)
1	60-100	Yearling (Y)
2	100-200	Sub –Adult (SA)
3	200 - >300	Adult (A)
EO	undetermined	Eyes Only (EO)

2.2.2 Data Analysis

Several statistical analyses were performed to identify trends and differences across the various river systems. Descriptive statistics, including mean and standard deviation, were computed to summarize the size class distribution for each river. A heatmap table was generated to visualize the concentration of different size classes across rivers, highlighting regions of higher or lower densities. Additionally, stacked bar charts were constructed to illustrate the proportional distribution of size classes within each river, offering insights into the relative abundance of juvenile and adult populations. Relative density was estimated using Equation 1 adapted by Bayliss (1987).

Equation 1:

$$\text{Density} = \frac{\text{Total number of crocodiles sighted}}{\text{Total distance of survey (km)}}$$

In addition to density estimates described above, the patterns of relative density of *C. porosus* over time in Sabah were assessed using secondary data collected from literature and internal reports provided by the Sabah Wildlife Department.

For the comparison of population trends with earlier studies, corrected density values were used to adjust the population estimates for direct comparison with two previous studies. This adjustment allowed for a standardized comparison across studies, despite the possibly differing sampling sites and distances covered. Correction factors adapted from Bayliss (1987) were introduced to correct the relative density to corrected density, following the methodology of Stuebing *et al.* (2002). This was done for the sole purpose of comparing the estimates of the current study to the previous study done in 1984 and 2002. Table 3.2 shows the correction factors adapted from Bayliss (1987). The corrected population density was estimated using Equation 2.

Table 2.2. Correction Factors based on size classes of individual crocodiles (Bayliss, 1987)

Class	Correction Factor
H	1.44
1	1.34
2	1.34
3	3.08
EO	6.54

Equation 2:

$$\text{Corrected Population Density} = \sum \frac{\text{(Number of Ind. per Class x Correction Factor per Class)}}{\text{Total Distance of Survey Area (km)}}$$

An ANOVA test was applied to determine whether there were statistically significant differences in population densities across the surveyed rivers. Prior to conducting the ANOVA, normality tests were performed to assess whether the data met the assumptions required for this analysis. Additionally, a line chart was created to illustrate the temporal trends in population size classes between 2017 and 2019.

To maintain consistency with previous studies, hatchlings were excluded from the analysis due to their low survival rates. The remaining size classes—yearlings, sub-adults, adults, and EO (Eyes Only)—were analysed to provide a more accurate depiction of population dynamics. The corrected density estimates were calculated for comparative purposes with these previous studies, though they do not reflect the true nature of population densities. As counts will fluctuate between surveys according to the number of animals present in the main river at that specific point in time, surveys were repeated for each river across three years, and the mean of these was used for final population density estimates.

2.3 Results

Between 2017 and 2019, *C. porosus* sightings were recorded across 10 rivers in Sabah, showing varying trends in population observations (Table 2.3). The Kinabatangan River consistently reported the highest number of sightings, with 156 sightings in 2017, which more than doubled to 463 in 2018, before slightly decreasing to 387 in 2019. Other rivers, such as Silabukan and Kalumpang, also showed relatively high sighting numbers, with Kalumpang peaking at 115 sightings in 2019. In contrast, rivers like Padas and Labuk had consistently low sighting numbers, with Padas recording only seven sightings in 2018. Overall, the total number of *C. porosus* sightings increased over the three years, rising from 472 in 2017 to 785 in 2019.

Table 2.3. Sightings of *C. porosus* in Sabah from 2017 to 2019 across 10 rivers.

River	**Average distance/year (KM)**	**Sightings**		
		2017	**2018**	**2019**
Klias	43	39	49	34
Padas	42	21	7	9
Kinabatangan	160	156	463	387
Silabukan	30	80	69	72
Segama	60	12	16	55
Bengkoka	55	22	18	28
Paitan	40	26	26	47
Kalumpang	48	63	42	115
Labuk	78	13	16	10
Serudong	53	40	21	28
Total		**472**	**727**	**785**

Distribution of *C. porosus* in Sabah

C. porosus densities across 10 rivers in Sabah were recorded from 2017 to 2019, revealing notable differences in population density among rivers and across years (Table 2.4). The highest average relative density was observed in the Silabukan River, with a mean density of 2.46 *C. porosus* per kilometre, followed closely by the Kinabatangan River, with 2.10 *C. porosus* per kilometre. In contrast, the Labuk and Padas Rivers exhibited the lowest densities, with average relative densities of 0.17 and 0.29 *C. porosus* per kilometre, respectively. Over the three-year period, the mean *C. porosus* density across all rivers was 0.85 *C. porosus* per kilometre in 2017, increasing to 0.93 in 2018 and further to 1.15 in 2019. This trend suggests a general increase in population densities, particularly in the Kinabatangan and Kalumpang Rivers, which showed consistent growth over time. The standard deviation values indicate high variability in densities, especially in 2019, when the range of densities between rivers was more pronounced.

A correlation analysis between *C. porosus* densities recorded in 2017, 2018, and 2019 demonstrates significant positive relationships between the years (all p-values smaller than 0.05), particularly between 2018 and 2019, with a correlation coefficient of 0.81 (Figure 2.3).

Table 2.4. *C. porosus* densities across 10 rivers in Sabah from 2017 to 2019.

River	Mean distance/year (KM)	Density			Mean Density
		2017	2018	2019	
Klias	43	0.91	1.14	0.79	0.95
Padas	42	0.50	0.17	0.21	0.29
Kinabatangan	160	0.98	2.90	2.42	2.10
Silabukan	30	2.67	2.30	2.40	2.46
Segama	60	0.20	0.27	0.92	0.46
Bengkoka	55	0.40	0.33	0.51	0.41
Paitan	40	0.65	0.65	1.18	0.83
Kalumpang	48	1.31	0.88	2.40	1.47
Labuk	78	0.17	0.21	0.13	0.17
Serudong	53	0.75	0.40	0.52	0.56
Mean Density		**0.85**	**0.93**	**1.15**	**0.97**
Standard Deviation		**0.73**	**0.94**	**0.92**	**0.79**

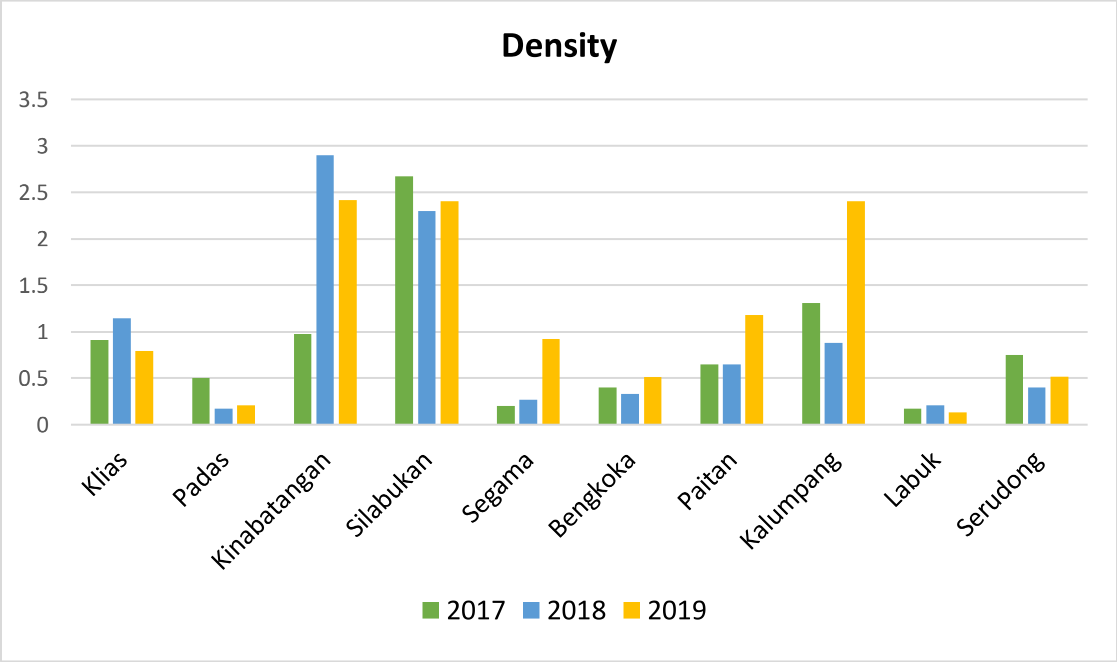


Figure 2.3. Correlation analysis between *C. porosus* densities in 2017, 2018, and 2019. Pearson's correlation coefficient for the comparison of 2017 and 2018 is 0.69, between 2017 and 2019 is 0.74 and between 2018 and 2019 is 0.81.

This indicates a stable and consistent trend in population densities estimates over time, where rivers with higher densities in one year tend to maintain or increase their crocodile populations in subsequent years. For instance, the Kinabatangan and Silabukan Rivers exhibited relatively high and stable densities throughout the study period. In contrast, rivers like Padas and Labuk showed low densities but remained consistent over time. The line chart comparing *C. porosus* densities across rivers highlights these patterns, with a noticeable upward trend in most rivers from 2017 to 2019. The increasing densities suggest that *C. porosus* populations in several rivers, particularly in larger systems like Kinabatangan, may be recovering or stabilizing.

While hatchlings are included in the above analysis, their survival rates are typically very low (around 10%). Hence, to account for this, Table 2.5 presents population densities with the hatchling group excluded, allowing for a more accurate representation of the population dynamics within the juvenile and adult size classes, which are more likely to contribute to long-term population growth and viability.

Table 2.5. Non-hatchling density of *C. porosus* in Sabah.

River	Non-Hatchling Density			Mean Density
	2017	2018	2019	
Klias	0.84	0.70	0.56	0.70
Padas	0.43	0.12	0.21	0.25
Kinabatangan	0.61	1.27	1.12	1.00
Silabukan	1.70	1.83	1.70	1.74
Segama	0.18	0.25	0.88	0.44
Bengkoka	0.40	0.22	0.38	0.33
Paitan	0.45	0.48	0.75	0.56
Kalumpang	0.56	0.42	1.52	0.83
Labuk	0.17	0.21	0.13	0.17
Serudong	0.49	0.17	0.26	0.31
Mean Density	**0.58**	**0.57**	**0.75**	**0.63**

The non-hatchling density of *C. porosus* shows notable variation between rivers and over the years 2017, 2018, and 2019. The highest densities were consistently observed in Silabukan, where the density remained stable at 1.70 to 1.83 *C. porosus* per kilometre over the three years. Similarly, the Kinabatangan River exhibited a significant increase from 0.61 in 2017 to 1.27 in 2018, followed by a slight decrease to 1.12 in 2019, highlighting this river's importance as a key habitat for non-hatchling crocodile populations. Other rivers, such as Kalumpang and Paitan, also demonstrated noticeable growth in non-hatchling density, particularly in 2019, when Kalumpang's density surged to 1.52 from lower values in previous years.

In contrast, Padas River and Labuk River consistently reported lower non-hatchling densities, with values as low as 0.12 in 2018 for Padas and 0.13 in 2019 for Labuk. Despite slight fluctuations, these rivers generally maintained low-density values throughout the study period. The overall mean density across all rivers showed a slight increase over time, from 0.58 in 2017 to 0.75 in 2019, indicating a general upward trend in non-hatchling *C. porosus* densities across the study area.

Population Structure of *C. porosus* in Sabah

The population structure of *C. porosus* in Sabah reveals variation across size classes, providing insights into the demographic composition and potential growth trends of the species in the region. Figure 2.4 provides a breakdown of the *C. porosus* population in Sabah by size class, based on density estimates.

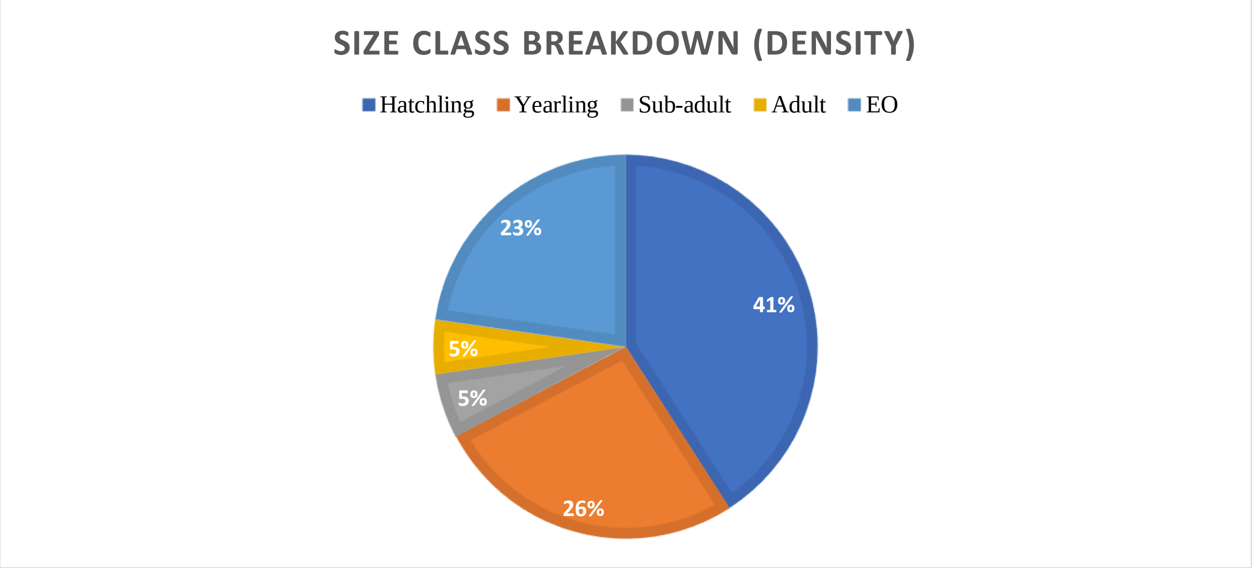


Figure 2.4. Population structure of *C. porosus* in Sabah by size class.

Hatchlings make up the largest portion of the population, with 0.45 individuals/km, representing 41% of all sightings. This is followed by yearlings, with 0.29 individuals/km, comprising 27% of the population. The "Eyes Only" (EO) category, which refers to individuals observed but not clearly identified by size class, accounts for 0.25 individuals/km, or 23%. Sub-adults, those approaching maturity, are at 0.06 individuals/km and represent 5% of the population, while fully grown adults make up 4%, with 0.05 individuals/km. This population structure suggests a relatively high proportion of younger individuals (hatchlings and yearlings), indicating successful reproduction.

Figure 2.5 illustrates the density of *C. porosus* across different size classes - hatchlings, yearlings, sub-adults, adults, and individuals recorded as "Eyes Only" (EO) from 2017 to 2019.

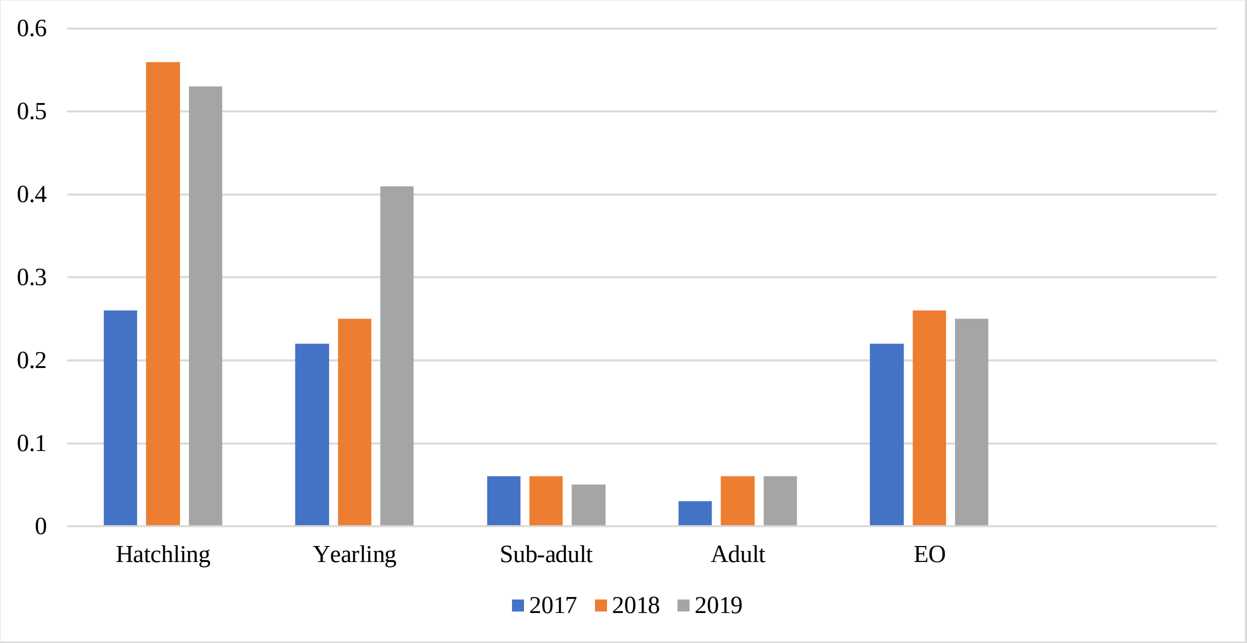


Figure 2.5. Density of *C. porosus* by Size Class (2017–2019).

Hatchlings consistently accounted for the largest number of sightings, with a noticeable increase from 2017 (0.26 individuals/km) to a peak in 2018 (0.56 individuals/km), followed by a slight decline in 2019 (0.53 individuals/km). Yearlings showed a similar pattern, with a moderate increase from 2017 to 2018, then levelling off in 2019. Sub-adult and adult sightings remained consistently low across all three years. Meanwhile, the "Eyes Only" remained relatively stable, with similar densities across all years.

For a clearer representation of the size class distribution and proportions of *C. porosus*, a 100% stacked area chart was constructed allowing for an easy comparison of how the relative proportions of different size classes have changed from 2017 to 2019 (Figure 2.6). By using proportions rather than absolute numbers, the chart provides insight into the shifting population dynamics and highlights the contribution of each size class to the overall population structure each year.

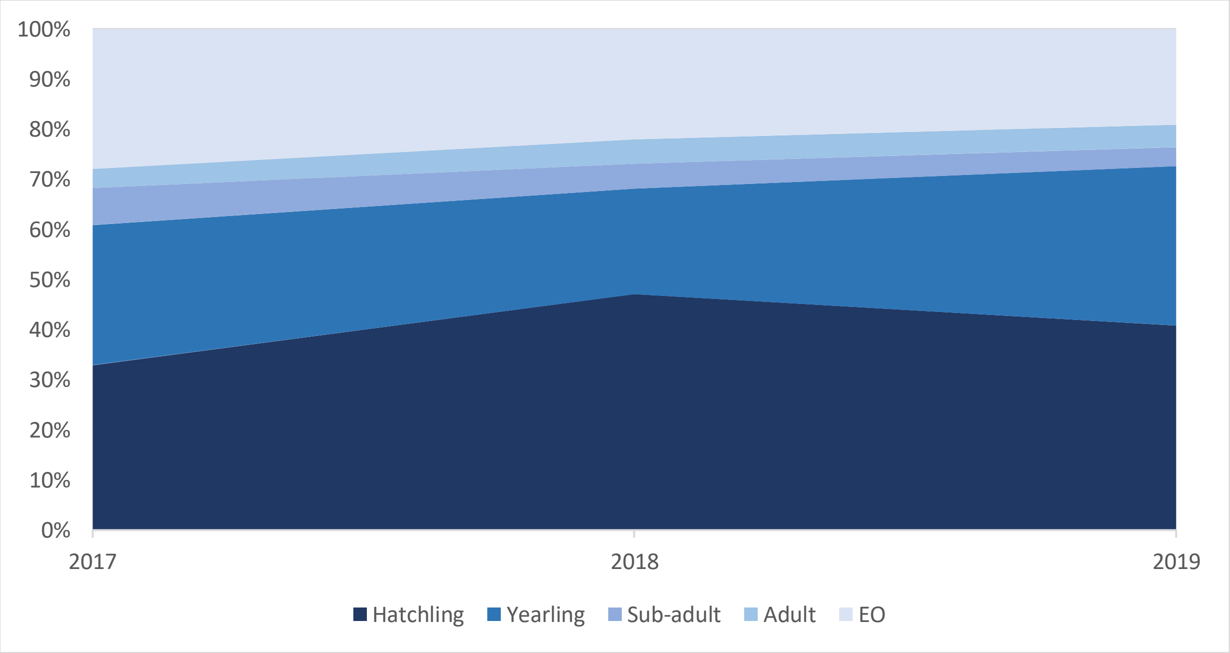


Figure 2.6. Proportional Changes in *C. porosus* Size Classes based on density from 2017 to 2019.

The hatchling class consistently represents the largest proportion, occupying almost 40% to 50% of the population across all three years. The proportion of yearlings remains relatively stable, fluctuating between 25% and 30%. Sub-adults, adults, and the EO category each contribute smaller proportions, with EO making up about 20% of the population, while sub-adults and adults contribute the least, together accounting for less than 15% of the total population. Overall, the chart highlights that the *C. porosus* population structure remains relatively stable over time, with hatchlings and yearlings dominating the population.

The mean size class distribution of *C. porosus* across all rivers in Sabah highlights some variation in population structure as shown in the heatmap table below (Table 2.6). The Kinabatangan River shows the highest mean number of individuals across all size classes, with a notable proportion of hatchlings (1.1 individuals/km) and yearlings (0.43 individuals/km), as well as substantial sub-adult and adult populations.

Similarly, the Kalumpang and Silabukan Rivers show moderate numbers of individuals across the juvenile classes, with 0.69 individuals/km of hatchlings and 0.42 individuals/km of yearlings in Kalumpang, and 0.7 individuals/km of hatchlings and 1.2 individuals/km of yearlings in Silabukan, indicating successful breeding activity and early survival in these rivers.

Table 2.6. Distribution of *C. porosus* size classes across rivers in Sabah (2017–2019): proportion by size class.

River	**Size Class (Mean Density)**				
	Hatchling	**Yearling**	**Sub-adult**	**Adult**	**EO**
Klias	0.28	0.19	0.14	0.05	0.3
Padas	0.05	0.07	0.02	0	0.17
Kinabatangan	1.1	0.43	0.09	0.1	0.38
Silabukan	0.7	1.2	0.1	0.17	0.3
Segama	0.02	0.27	0	0	0.17
Bengkoka	0.07	0.13	0.05	0.02	0.15
Paitan	0.28	0.28	0.03	0.05	0.2
Kalumpang	0.69	0.42	0.04	0.02	0.33
Labuk	0	0.05	0.01	0	0.1
Serudong	0.25	0.08	0.04	0.06	0.15

🟦 High proportion

🟥 Low proportion

In contrast, rivers, such as Labuk, Padas, and Segama, exhibit much lower mean numbers across all size classes, particularly in the sub-adult and adult categories. Padas and Labuk have a mean of 0 adults, and Segama has no recorded sub-adults or adults. The EO (Eyes Only) category shows considerable variation between rivers, with Kinabatangan (0.38 individuals/km) and Kalumpang (0.33 individuals/km) recording the highest densities, while Labuk recorded the lowest density (0.1 individuals/km).

A stacked bar chart was created as supplementary data, providing a clear visualization of the distribution of *C. porosus* size classes across various rivers in Sabah (Figure 2.7). The chart shows differences in population structure between the rivers, with Kinabatangan standing out as an important habitat for juveniles. In Kinabatangan, hatchlings dominate the population, followed by yearlings and EO (Eyes Only) observations. The large proportion of juveniles in Kinabatangan underscores its importance as a breeding and nursery site, supporting the early life stages of *C. porosus* in greater numbers compared to other rivers.

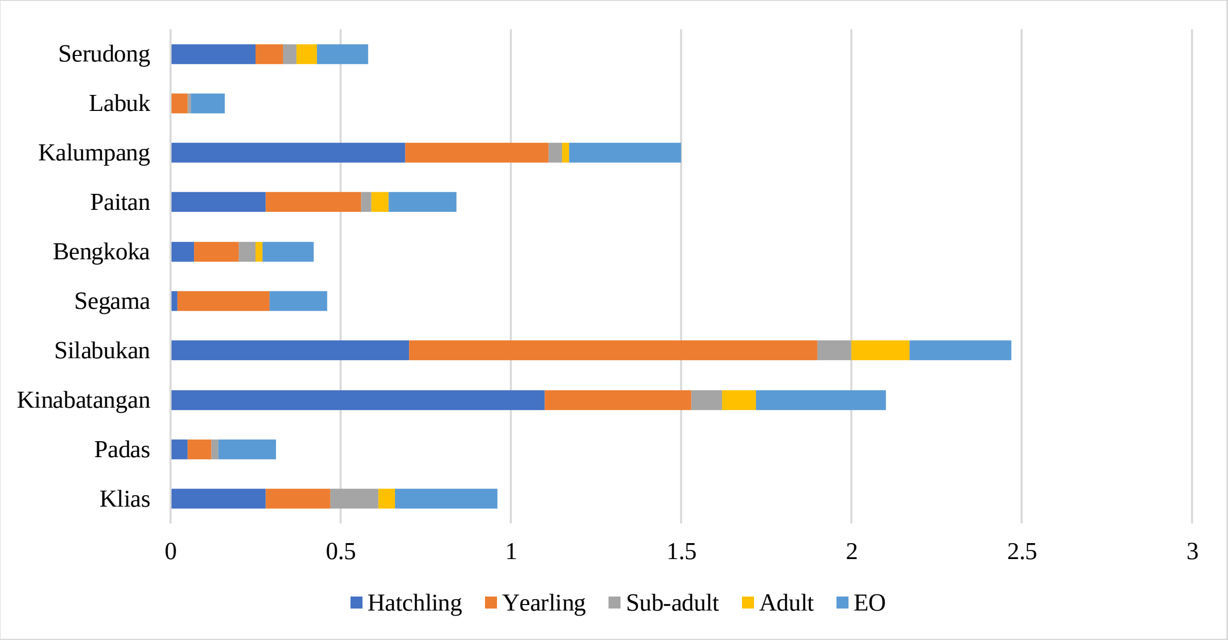


Figure 2.7 Distribution of *C. porosus* size class across 10 rivers in Sabah.

In contrast, rivers like Padas, Labuk, Bengkoka and Segama exhibit much smaller populations, with very few individuals recorded across all size classes.

To further assess the population structure of *C. porosus* in each river, a proportion stacked bar was created to visualize the differences between hatchling and non-hatchling densities (Figure 2.8).

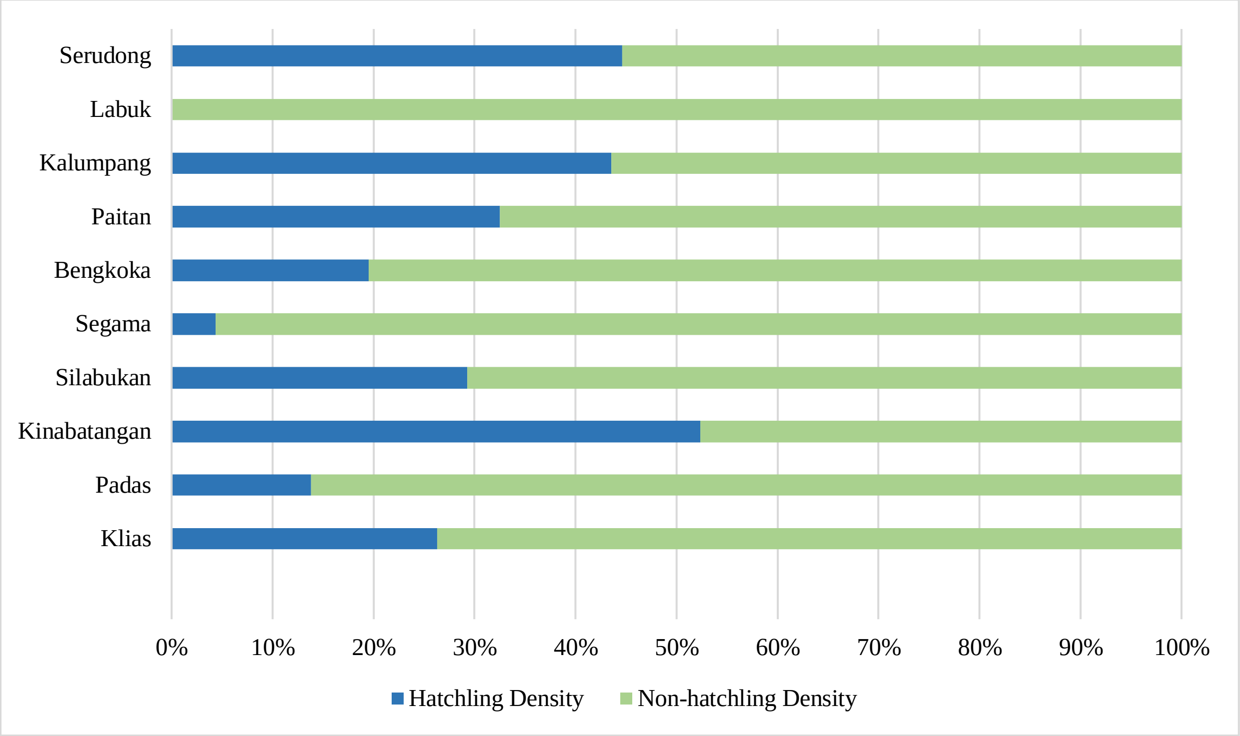


Figure 2.8. Proportional distribution of hatchling and non-hatchling densities across 10 rivers in Sabah.

Kinabatangan shows the most equal proportion of hatchling to non-hatchling density, with hatchlings making up over 50% of the total crocodile population and non-hatchlings making up approximately 47%. In contrast, rivers like Labuk and Segama exhibit very high non-hatchling proportions, 100% and 95%, respectively, while hatchlings represent 0% to 5% of the total population. All the other rivers show a higher proportion of non-hatchling density, with hatchlings contributing around 15-45% of the total population.

Population trend of *C. porosus* in Sabah

In this analysis of the *C. porosus* population trend, hatchlings were excluded to avoid noise in the data due to their high mortality rates and to maintain comparability with previous studies (Table 2.7). By focusing on the juvenile and adult classes, this comparison provides more reliable insights into the population dynamics. The corrected density estimates, derived for comparative purposes, do not represent the actual population density but offer a consistent method for analysing changes over time in Sabah's *C. porosus* population.

Table 2.7. Corrected Density (CD) of C. *porosus* population in Sabah.

Survey	Distance surveyed (km)	Class*				No of encounters	Density/km	Corrected density/km
		1	2	3	EO			
Whitaker, 1984	1146.0	13	9	3	31	56	0.05	0.21
Stuebing *et al*. 2002	222.8	178	29	3	31	241	1.10	2.27
Present 2017-2019	609.0	178	34	30	147	389	0.64	2.19

* Class 1 = Yearling; Class 2 = Sub-adult; Class 3 = Adult; EO = Eyes only. Correction factors adapted from Bayliss (1987): Class 1 CF = 1.44; Class 2 CF = 1.36; Class 3 CF = 2.17; EO CF = 6.54

The corrected density table highlights population estimates across three studies: Whitaker (1984), Stuebing *et al.* (2002), and the current study (2017-2019). Whitaker's survey, conducted over a large distance of 1146 km, revealed a low corrected density of 0.21 individuals per km. In contrast, Stuebing *et al.* (2002), surveying 222.8 km, showed a significantly higher corrected density of 2.27 individuals per km, indicating a potential population increase in the decades following Whitaker's study. The current study, covering a distance of 609 km, revealed a corrected density of 2.19 individuals per km, closely aligning with Stuebing *et al.*'s findings suggesting relative population stability since 2002. However, the observed differences between Whitaker's earlier study and the more recent surveys underscore the potential increase in *C. porosus* populations in Sabah.

2.4 Discussion

The results of this study indicate that *C. porosus* populations exist in the waterways of Sabah. There were sightings of *C. porosus* in all the rivers surveyed although the results suggest a relatively high number of crocodiles in certain river systems such as Silabukan River, Kinabatangan River, and Kalumpang River and highly restricted and potentially vulnerable populations in others such as in Padas River and Labuk River which had consistently low sightings throughout the years.

Distribution of *C. porosus* in Sabah

The sightings data across rivers in Sabah from 2017 to 2019 reveal notable variation in *C. porosus* populations, with significant differences observed between the rivers surveyed. Kinabatangan, for example, stands out with consistently high sightings, particularly in 2018 when 463 individuals were recorded. The relatively stable and high population in this river may be attributed to its vast size and diverse habitat types, which provide ample nesting and feeding grounds for crocodiles of various life stages. Additionally, most individuals were easy to approach, indicating that crocodiles are well adapted to the presence of humans in the area. This observation is quite different from what was observed in the *C. porosus* study conducted in the Kinabatangan River in 1984. It was observed that the crocodiles were shy and hard to approach during the survey due to possible hunting pressure.

The findings from various studies on the relationship between river size, habitat diversity, and crocodile populations can be directly linked to the situation in the Kinabatangan River in Sabah. As one of the largest and most diverse river systems in the region, the Kinabatangan supports a wide array of habitats, including freshwater swamps, oxbow lakes, mangroves, and vast floodplains. These varied environments create an ideal ecosystem for *C. porosus*, as they provide crucial resources such as nesting sites, basking areas, and abundant prey, similar to the findings of Fukuda *et al*. (2013) in the Ord River system. The extensive reach of the Kinabatangan, combined with its rich ecological diversity, is likely a key factor behind the high crocodile sightings reported in this study.

Just as Thorbjarnarson (1992) observed in the Orinoco River system, the diverse habitats of the Kinabatangan offer safe havens for juvenile crocodiles and important nesting areas for adults. This combination of ecological niches supports not only *C. porosus* but also a broad range of other wildlife species, contributing to the overall health and stability of the ecosystem. The presence of oxbow lakes and wetlands within the Kinabatangan, similar to those studied in Zimbabwe by Hutton (1987), further reinforces the river's role as a biodiversity hotspot, supporting both large predator populations and their prey. These studies collectively highlight the importance of habitat diversity and river size in sustaining healthy populations of crocodiles and other wildlife, which is clearly evident in the *C. porosus* population in Kinabatangan River.

In contrast to Kinabatangan River, rivers like Padas and Labuk show lower sightings across all three years. Padas River is surrounded by a predominantly hilly landscape, with parts of the river running through dense rainforest. Much of the river's surrounding environment is uneven, and in some areas, the steep terrain creates fast-moving waters, which is not suitable for crocodile habitation. Additionally, the land around the river is subject to agricultural activities and human encroachment, potentially leading to habitat degradation. The low sightings of *C. porosus* in the Padas River could be attributed to these environmental factors. Crocodiles generally prefer slower-moving, calmer waters with access to wetlands, floodplains, or backwaters that offer suitable nesting sites and abundant prey.

Labuk River flows through a region that includes both coastal mangroves and inland lowland forests. While some portions of the river feature mangrove ecosystems that are hypothetically suitable for *C. porosus*, much of the surrounding landscape has been heavily impacted by agricultural activities, particularly palm oil plantations that has led to significant habitat fragmentation and degradation. Additionally, human encroachment and increased disturbance along the riverbanks may contribute to the crocodiles' avoidance of these areas, further reducing the likelihood of sightings in this river. Rivers with greater human activity tend to experience lower crocodile populations, as seen in the Tarcoles River in Costa Rica, where human encroachment has led to significant population declines (Venegas-Anaya *et al*., 2015).

Silabukan and Kalumpang Rivers, both exhibiting moderate crocodile sightings, share several environmental characteristics that support their *C. porosus* populations. Both rivers offer a mix of coastal mangrove ecosystems and freshwater habitats that provide suitable environments for nesting and juvenile crocodile development. Despite these favorable conditions, human activities such as agriculture and logging have led to habitat fragmentation in both areas, limiting the full potential of these rivers to support larger populations. Mangroves near the river mouths still serve as critical habitats, especially for juveniles, which may explain the moderate sightings reported in both rivers.

Bengkoka River, while located in a less populated region of northern Sabah, exhibits low crocodile sightings, which may be attributed to a combination of environmental and human factors. The river's relatively narrow width and dynamic, fast-moving sections limit the availability of suitable habitat for *C. porosus*. Additionally, significant human activities observed during the surveys, including heavy fishing and the presence of large tankers, likely disrupt the river's natural ecosystem and further reduce its attractiveness as a habitat for crocodiles. The constant traffic and disturbance from tankers, combined with the depletion of potential prey due to intense fishing, may have driven *C. porosus* away from this river, explaining the low number of sightings recorded. These factors collectively hinder the river's capacity to support a stable crocodile population.

The year-to-year trend showing a general increase in crocodile sightings between 2017 and 2019, could be attributed to natural fluctuations in *C. porosus* behavior and environmental conditions. One possible explanation is that variations in seasonal water levels and rainfall patterns could have concentrated crocodile populations in smaller, more accessible areas of the rivers during the surveys. In years with lower water levels, crocodiles are more likely to be found in shallower, more confined sections of rivers, making them easier to spot during surveys. Similar trends have been observed in other studies, where fluctuations in water availability directly influenced the detectability of crocodiles. For example, Hutton & Woolhouse (1989) found that in Zimbabwe, Nile crocodiles exhibited significant seasonal fluctuations in population density and sightings, particularly during the dry season when water levels dropped, concentrating both crocodiles and their prey into smaller, more accessible areas. This led to higher crocodile sightings in certain months, while during the wet season, crocodiles were more dispersed, making them harder to detect.

A similar trend was observed in the Ord River system in Australia, where Fukuda *et al*. (2013) found that seasonal changes in water flow and prey availability directly affected *C. porosus* behavior and distribution. During the wet season, crocodiles moved into more remote areas, following prey availability, while during the dry season, they were more concentrated along permanent water bodies, making them easier to spot during surveys. These findings were also echoed by Thorbjarnarson (1999), who noted that in Venezuela, the Orinoco crocodile (*C. intermedius*) exhibited seasonal movements linked to water availability and prey concentrations.

Even though C. *porosus* are salt-tolerant species, it was observed that their site distribution reduced as salinity increased and are not likely to occupy rivers that are wide and of extreme salinity. This observation is consistent with the findings of Than *et al*. (2020) where it was noticed that site occupancies of crocodiles reduced with increasing salinity. There were very few sightings of *C. porosus* in river sections closer to the mouth of the sea. These sections of river were mostly observed to be wider with high tides and close to no vegetation along the banks. The individuals sighted in this study were more commonly seen in river creeks and tributaries that are of narrow river canals, especially in rivers located in wildlife sanctuaries like Kinabatangan River. In the same way, a study on the American crocodile in Florida found that crocodiles utilize narrow channels and creeks to access inland freshwater habitats such as mangroves or potential nesting sites (Mazzotti *et al.*, 2007).

Results from previous studies on the ecology of *C. porosus* also indicate that low-salinity areas which are usually further away from sea mouth are commonly used by foraging and nesting individuals (Fukuda & Cuff, 2013; Evans *et al.*, 2017). According to Grigg *et al*. (1980), the relative density, hatchling growth and survival rates of *C. porosus* are constrained in areas of higher salinity. A study on the response of fishes to physiochemical changes in mangroves in Florida revealed a significant association between salinity and aquatic productivity (Lorenz, 1999). The higher the salinity (closer to sea mouth), the lower the aquatic productivity. Consequently, there is a higher abundance of terrestrial prey upstream where aquatic productivity is high. This possibly explains the distribution and occupancy of *C. porosus* further away from the sea mouth as crocodiles are known to consume more terrestrial prey than marine prey (Adame *et al*., 2018).

While sightings data deliver valuable baseline information on the presence of *C. porosus* across various rivers, they are not adequate to estimate population size precisely. Sightings are influenced by several factors, including detection biases, habitat accessibility, and crocodile behavior, all of which can lead to underestimation or overestimation of actual population sizes. For instance, individuals that are submerged or concealed by vegetation are often missed during surveys, while environmental conditions such as water levels and visibility can affect detection rates (Bayliss *et al*., 1986).

For instance, in the study of American alligators in Florida, Fujisaki *et al*. (2011) observed that detection rates were strongly influenced by environmental factors such as water clarity and vegetation cover. Alligators were more easily detected in open water habitats than in dense marshes, which led to potential underestimation of the population size. Fujisaki *et al*. (2011) emphasized the importance of combining sightings with density estimates to account for habitat-specific biases.

Another example comes from the study of *C. porosus* populations in Northern Australia by Webb *et al.* (2000), where sightings fluctuated significantly depending on water levels and the time of year. During the dry season, crocodiles were more concentrated in remaining water bodies, making them easier to detect, whereas during the wet season, they dispersed across a wider area, reducing detection ability. The differences in habitat structure during seasonal fluctuations such as the availability of sandbanks and slow-moving waters also affect detectability. This demonstrates how using sightings alone can misrepresent true population size, particularly if surveys are conducted during periods of low visibility or crocodile activity.

In contrast, density estimates provide a more reliable and accurate measure of population size, particularly in studies involving elusive species such as *C. porosus*. This is because density estimation methods employ systematic sampling techniques that accounts for distance, for example, as a variable, leading to more comprehensive assessments. This technique allows researchers to estimate animal densities even in cases where individual identification is difficult, integrating data from multiple sources to improve the precision of estimates (Webb *et al.*, 2000; Fujisaki *et al.*, 2011). These methods are especially valuable for species like *C. porosus*, where visibility and detection can vary significantly due to factors such as water levels and habitat complexity.

The density results from this study demonstrates that some rivers exhibit higher *C. porosus* densities than others, with Silabukan having the highest density of *C. porosus* at 2.46 individuals per kilometre, suggesting that this river provides an optimal habitat for crocodiles, likely due to the availability of calm waters, suitable nesting areas, and the prohibition of activities such as logging and land conversion (Sabah Forestry Department). High densities in rivers like Silabukan are consistent with other studies, such as Thorbjarnarson (1992), who observed that diverse river ecosystems with abundant prey and nesting sites supported higher crocodile populations, particularly in Venezuela's Orinoco River. In areas where habitat remains relatively intact, like in Silabukan, crocodile densities thrive, highlighting the importance of habitat diversity in population sustainability.

In comparison, the Kinabatangan River, which is one of the largest and most ecologically diverse rivers in Sabah, recorded slightly lower densities than Silabukan, although it remains a key habitat for *C. porosus*. The *C. porosus* density in Kinabatangan, while still large, reflects the balance between its diverse habitats and the impact of increasing human activities along the river. A study by Webb *et al*. (2000) found that crocodile populations in Northern Australia exhibited lower densities in areas with more human disturbance, despite favourable environmental conditions. This is consistent with the findings from Kinabatangan, where human presence may be limiting the full potential for higher crocodile densities.

Rivers like Padas and Labuk on the other hand, recorded much lower densities, with values well below those of Silabukan and Kinabatangan. These low densities, potentially linked to habitat degradation and increased human activities such as agriculture and development (Sabah Forestry Department), are similar to findings from other regions where human encroachment has led to declining crocodile populations. Campbell *et al*. (2015) noted that human activities near crocodile habitats, including pollution and habitat fragmentation, were directly associated with low population densities, a pattern that is evident in these rivers.

An example of exceptionally low crocodile density was found in Vietnam, where the Siamese crocodile (*C. siamensis*) population is critically threatened. In certain regions, surveys documented densities as low as 0.06 individuals per kilometer (Bezuijen *et al.*, 2013). This species is classified as critically endangered on the IUCN Red List, primarily due to severe habitat degradation, poaching, and increased human activity. These very low densities emphasize the difficulties faced by the species, with many populations now confined to fragmented and isolated habitats. This situation mirrors broader trends in Southeast Asia, where *C. siamensis* faces significant challenges to its survival, making it one of the most threatened crocodilian species globally.

Although *C. porosus* populations are listed as Least Concern by the IUCN globally, particularly in regions like Australia where populations have rebounded after near-extinction levels due to hunting (Webb *et al.*, 2000), the situation for *C. porosus* is not without its challenges. In Sabah, while relatively healthy populations are recorded in rivers such as Kinabatangan and Silabukan, there remain localized threats such as habitat fragmentation from palm oil expansion, pollution, and illegal poaching that could lead to population declines if not properly managed (Jalil, 2016).

As mentioned earlier, the densities of *C. porosus* in the Silabukan and Kinabatangan rivers are the highest recorded in this study. However, these figures are still relatively low when compared to crocodile populations in other regions, particularly in Australia, where much larger populations have been documented. For example, in the Northern Territory of Australia, Fukuda *et al.* (2007) reported densities of up to 5.6 individuals/km in certain parts of the Mary River. Similarly, Webb & Manolis (1989) found densities of *C. porosus* of over 10 individuals/km in smaller rivers and billabongs in Northern Australia, where habitat conditions are optimal and human disturbance is minimal.

Further comparisons can be drawn from a study in Papua New Guinea, where *C. porosus* densities in their rivers were found to range between 3.8 and 6.5 individuals/km, particularly in less disturbed areas with abundant prey and suitable nesting sites (Hollands, 1987). These figures show that while the densities observed in Silabukan and Kinabatangan rivers indicate healthy populations, they are still much lower than what has been recorded in other countries with larger or less disturbed *C. porosus* populations. Having said that, the higher crocodile densities in regions like Northern Australia are often found in protected areas where conservation efforts have allowed crocodile populations to recover more robustly after decades of hunting pressure (Fukuda *et al.*, 2007).

Population structure of *C. porosus* in Sabah

Understanding the density differences between hatchlings and non-hatchlings provides key insights into the reproductive success and survival rates of *C. porosus* populations across the surveyed rivers. Hatchling densities are a great indicator of breeding activity and successful nesting, while non-hatchling densities (including juveniles, sub-adults, and adults) reflect survival rates beyond the early life stages. By comparing the densities of these two groups, the health and sustainability of populations can be assessed.

The Kinabatangan River, which shows an almost equal proportion of hatchling (53%) and non-hatchling (47%) densities, indicates that the river provides suitable breeding conditions, as well as favourable habitats that support the survival of bigger individuals. The high hatchling density suggests successful reproduction, which likely reflects the availability of nesting sites, and optimal environmental conditions for nesting and hatching. Studies such as Fukuda *et al.* (2013) in Northern Australia show that higher hatchling densities correlate with areas where riverine habitats provide safe nesting environments and adequate food sources for hatchlings.

In contrast, rivers like Labuk, Segama, Bengkoka and Padas, where non-hatchling densities are overwhelmingly dominant (95-100%), indicate that while survival rates of older crocodiles may be high, the breeding success in these rivers is likely low. This could be due to a variety of factors, including the lack of suitable nesting sites, increased predation on nests, or human activities that disturb breeding habitats. Similar findings have been reported by Thorbjarnarson (1999) in the Orinoco River, where high adult densities but low hatchling densities were attributed to habitat degradation and increased human disturbance during the breeding season.

It is also possible that much of the river sections surveyed in these rivers have higher salinity levels compared to other rivers, which could influence *C. porosus* nesting and population dynamics. These rivers are primarily used for fishing and transportation, unlike other surveyed rivers, which are frequently utilized by local villagers for activities such as bathing, swimming, and washing. The higher salinity levels along most of these rivers make them less suitable for these activities. A study on the American crocodile in Florida's Everglades National Park supports the idea that salinity plays a crucial role in crocodile nesting success. Mazzotti *et al*. (2007) found that the number of nesting crocodiles increased significantly after a canal was plugged to retain fresh water in the park, reducing saltwater intrusion. The lowered salinity levels created more favourable nesting conditions, leading to improved hatchling growth and survival. This suggests that high salinity in the surveyed sections of Labuk, Segama, Bengkoka, and Padas Rivers may similarly reduce the suitability of these habitats for successful *C. porosus* nesting and juvenile development

The other rivers, which exhibit intermediate proportions of hatchling densities (15-45%), suggest varied breeding success and survival rates. In rivers like Silabukan and Kalumpang, where hatchling densities are higher, it is evident that these rivers provide some degree of favourable breeding conditions, but the lower proportion of non-hatchlings could indicate challenges in long term survival. This is consistent with research by Webb & Manolis (1989) in Northern Australia, where factors such as predation, and habitat fragmentation were found to impact the transition of hatchlings to juvenile stages. In regions where juvenile mortality is high, even rivers with strong hatchling production may not see significant increases in adult populations without conservation interventions. Silabukan River and Kalumpang River share several ecological characteristics that likely contribute to their higher hatchling densities compared to the other seven rivers in this study

These rivers are large and have a diverse range of aquatic and riparian habitats, including oxbow lakes, wetlands, and stretches of low-lying floodplains. These features provide ideal nesting and basking areas for *C. porosus* and are beneficial to breeding females. Additionally, the presence of sandy and vegetated riverbanks makes the environment suitable for nest construction and hatchling survival as water level remains stable in these conditions. These areas provide the required conditions for temperature regulation of nests, which is critical for egg development. Webb *et al.* (1983) observed that nesting of *C. porosus* occurs in areas characterized by dense vegetation or sandy banks. The study found that nesting success was significantly higher in sites with dense vegetation cover, which also reduced predation risk. In addition to nesting sites, hatchling habitats are equally important for the initial survival of crocodiles. Hatchlings require shallow, calm waters with a lot of cover, such as submerged vegetation or mangroves, where they can hide from predators and have access to food sources like small fish and invertebrates.

The variation in non-hatchling densities across the rivers could also be attributed to environmental factors and human activities. In areas like Bengkoka, where fishing activities and the presence of large tankers were observed, the disturbance to crocodile habitats may be limiting the survival of juveniles and adults. Similar observations were made by Fukuda *et al.* (2013) in Northern Australia, where human activities near river systems were associated with lower non-hatchling densities, despite healthy hatchling production.

Cott (1961) and Graham (1968) suggested that in an environment free from human interference, a normal crocodile population should primarily consist of adults, with hatchlings representing a smaller proportion. This pattern is attributed to natural survival dynamics, where older, larger individuals dominate due to their better survival rates, while the smaller individuals face higher mortality. Additionally, the population structure can fluctuate based on the time of year, as breeding typically occurs during the wet season, leading to a temporary increase in hatchlings and juveniles during certain periods.

Contrary to these findings, Wallace *et al.* (2013) proposed a different model for a stable crocodile population based on their study of *C. niloticus* in the lower Zambezi Valley. They concluded that a stable population is characterized by a high proportion of smaller individuals, with fewer large adults. This structure indicates ongoing reproduction and recruitment into the population, suggesting that a healthy crocodile population should have a strong representation of younger individuals as a sign of future growth.

In comparison to the current study in Sabah, certain rivers such as Kinabatangan and Kalumpang, which show a relatively balanced proportion of hatchlings and non-hatchlings, align more closely with Wallace *et al*.'s (2013) definition of a stable population. However, rivers like Labuk and Segama, where non-hatchlings dominate the population, may reflect the patterns described by Cott (1961) and Graham (1968), indicating that environmental pressures or human impacts might be influencing population structure. These differences highlight the need for localized conservation strategies.

C. porosus has a relatively low hatchling survival rate, making its management and monitoring particularly crucial (Brien *et al*., 2014). Hatchlings tend to inhabit a range of environments, including rivers, freshwater, and brackish marshlands. In Sabah, river Kinabatangan, Serudong and Kalumpang, appear to be especially favourable for nesting and reproduction, with most hatchlings being distributed upstream and in tributaries. Very few were observed near river mouths, suggesting that these zones may not be optimal for young crocodiles. It has been suggested by Grigg (1981) that freshwater environments provide physiological advantages to hatchlings by increasing the efficiency of osmoregulatory processes, helping them conserve energy during a critical life stage.

Additionally, Webb *et al*. (1983) highlighted the importance of freshwater access for adult females, particularly for shell deposition during egg development. Crocodiles also require open canopy areas to regulate the temperature of their nests and eggs, which is essential for successful reproduction (Vitt & Caldwell, 2014). Furthermore, ontogenetic diet shifts (changes in an animals' diet as it grows), territorial behaviour, and predation pressures often lead crocodiles at different life stages to occupy distinct habitats. Delaney & Abercrombie (1986) pointed out that these factors strongly influence the selection of habitat, with younger crocodiles seeking refuge in less contested, safer areas to avoid predation and territorial aggression from larger adults.

Generally, in reptile population studies, the hatchling-to-non-hatchling density ratio is a crucial measure of population health, providing insights into reproductive success, juvenile survival, and the overall balance between younger and older individuals. A high proportion of hatchlings generally reflects successful breeding, indicating that the environment offers adequate nesting sites and suitable conditions for egg incubation (Mazaris *et al.*, 2005). On the other hand, if there is a low number of non-hatchlings, this could signal challenges in juvenile survival, often caused by predation, habitat degradation, or limited prey availability (Hutton, 1987). A balanced ratio, where both hatchlings and non-hatchlings are well represented, typically points to a stable and healthy population, with effective recruitment of individuals into older age classes (Fukuda *et al.*, 2007).

For example, Mazaris *et al.* (2005) found that a higher proportion of hatchlings in Mediterranean loggerhead turtle (*Caretta caretta*) populations corresponded with successful nesting but also highlighted the importance of juvenile and adult survival for population stability. A skewed ratio towards hatchlings without a corresponding number of non-hatchlings can signal threats like high predation rates or human interference during early life stages.

Another example of how hatchling-to-non-hatchling ratios are used to assess population health can be found in studies on American alligator populations. Woodward *et al.* (1995) documented that a high proportion of hatchlings relative to juveniles and adults in certain areas of the Everglades indicated strong reproduction rates. At the same time, high predation rates on hatchlings and juveniles, as well as habitat degradation, were limiting the recruitment of young individuals into older age classes. A skewed ratio, with many hatchlings but fewer juveniles and adults, indicated that despite high reproductive output, the population faced threats that could impact its long-term stability if survival rates did not improve.

In conclusion, the ratio of hatchlings to non-hatchlings plays a vital role in evaluating the health and sustainability of reptile populations, including *C. porosus*. A balanced ratio, where both hatchlings and non-hatchlings are well-represented, indicates successful reproduction and juvenile survival, suggesting a stable and thriving population. For future conservation efforts, monitoring the hatchling-to-non-hatchling ratio provides essential insight into population dynamics and helps identify areas where intervention is needed. Understanding these dynamics will be critical for shaping targeted conservation strategies aimed at mitigating threats and promoting sustainable crocodile populations in diverse habitats.

Population trend of *C. porosus* in Sabah

Corrected density estimates from three different surveys, including Whitaker (1984), Stuebing *et al.* (2002), and the present study (2017-2019), provides a comparative overview of the changes in *C. porosus* population densities over time. While this offers a useful tool for comparison, correction factors need to be tailored to the specific environment in which they are applied. The correction factors used in these studies were adapted from Bayliss (1987), whose research was designed specifically for Australian conditions, which differ from the local riverine environments and do not fully account for the ecological and environmental variations between Australia and Sabah.

In Northern Australia, rivers tend to be wider and less vegetated, providing better visibility during surveys (Fukuda *et al.*, 2013). In Sabah, many rivers are narrower and heavily vegetated, which can reduce visibility and make crocodile sightings more challenging. These differences suggest that the correction factors from Bayliss' study may overestimate or underestimate the actual crocodile densities in Sabah, depending on how well they account for these environmental factors.

Furthermore, the increase in corrected densities between 1984 and the more recent surveys in 2002 and the present study may reflect a combination of factors, including improved survey methods, increased observer experience, and potentially higher population densities due to conservation efforts or habitat changes. As noted by Bayliss (1987), visibility biases must be adjusted based on local conditions, and using generalized correction factors across different regions may lead to inaccurate estimates.

Developing correction factors that are suited to a specific local environment is a highly complex process that requires years of study, as it involves understanding the unique ecological and environmental conditions of a region, such as water clarity, vegetation density, and the behaviour of the species in question. Because of the time and resources required, correction factors were not developed for this study. However, the use of density estimates, without correction for visibility biases, still provides a reliable tool for assessing the population status of *C. porosus*. While density estimates might not account for every factor that could influence sight ability, they give a clear indication of population trends and overall abundance, making them a valuable method for conservation management and comparison across different regions (Webb & Manolis, 1989). This approach ensures that researchers can still derive meaningful insights into population status, even without the development of locally-tailored correction factors.

While locally developed correction factors provide a more refined estimate of crocodile densities, many studies have shown that density estimates are still highly effective for evaluating population trends and health, particularly when tailored correction factors are unavailable. For instance, in a study on *C. niloticus* in the Okavango Delta, Southern Africa, Wallace *et al.* (2011) relied on density estimates to assess population dynamics, despite the absence of locally developed correction factors. They found that density estimates provided robust data on population structure and trends over time, which was valuable for conservation planning. Similarly, in Papua New Guinea, Hollands (1987) used density estimates to monitor *C. porosus* populations and found that they provided a reliable snapshot of population health.

Additionally, the use of density estimates allows researchers to make immediate assessments without the delays inherent in developing and validating correction factors over many years. As these examples show, density data serves as a solid foundation for understanding population trends, even if they do not account for every bias. The key advantage is that densities can still reflect significant shifts in population size, helping conservationists prioritize areas for action. While the development of correction factors remains the ideal goal, relying on densities offers a practical and effective interim solution for monitoring *C. porosus* in Sabah’s diverse river systems.

In reptile population studies generally, density estimates have been widely acknowledged as a valuable tool, especially in situations where developing specific correction factors is unfeasible. Rodda *et al*. (2001) demonstrated the effectiveness of this method in monitoring the brown tree snake population trends in the Mariana Islands. While it was acknowledged that density estimates were not perfect, this approach still provided crucial data for conservation efforts of the reptile

Similarly, Pike *et al.* (2008) discussed the use of density estimates in lizard populations, noting that while these estimates do not account for all biases (such as visibility), they remain essential for tracking population changes over time. The study showed that even with limited data correction, density estimates provided reliable indication of the broad-headed snake population, which was crucial for implementing their conservation strategies. These studies reinforce the idea that, while correction factors tailored to specific environments enhance accuracy, the use of density estimates offers a flexible and practical alternative for understanding reptile population trends in various ecological contexts.

In conclusion, factors such as habitat quality, prey availability, predation pressure, and human impact play critical roles in determining crocodile population densities. Rivers with diverse ecosystems, abundant prey, and minimal human disturbance tend to support higher densities of crocodiles as compared to heavily disturbed or prey-limited rivers, which show lower densities. Understanding these factors is crucial for developing effective conservation strategies aimed at maintaining or enhancing *C. porosus* populations across their range.

Based on the analysis of *C. porosus* populations across the surveyed rivers in Sabah, it is evident that some rivers require more urgent conservation efforts than others. Rivers like Labuk, Segama, Bengkoka, and Padas show low densities of hatchlings and non-hatchlings, indicating potential issues such as habitat degradation, high salinity, and limited prey availability. These factors suggest that these rivers are not providing adequate conditions for successful breeding and survival. On the other hand, rivers such as Kinabatangan, Silabukan, and Kalumpang exhibit relatively healthy and stable *C. porosus* populations, with balanced hatchling and non-hatchling densities. These rivers, with their diverse habitats and abundant prey, provide critical nesting sites and favourable environments for crocodile survival. While these rivers show stability, continued conservation efforts are necessary to maintain their current status, especially given ongoing threats like habitat encroachment and human activities. Prioritizing efforts in the more vulnerable rivers while ensuring the stability of healthier populations will be key to safeguarding *C. porosus* populations across Sabah.

The differing densities and population structures observed in each river throughout this study highlight the importance of developing region-specific or even river-specific management strategies for *C. porosus* populations in Sabah. Accurately identifying population changes is challenging due to biases in accessibility and detectability, which can skew estimates. While generalized models to derive correction factors may assist in future research, their value is limited when the underlying causes of population trends are not fully understood. As Webb & Smith (1987) suggest, population estimates must be supplemented with other demographic variables such as survival rates and reproductive success. Additionally, population shifts within river systems may be a spatial response to environmental changes, making it essential to combine demographic data with spatial analyses to develop reliable models for predicting future population dynamics.

CHAPTER 3
Habitat Use and Movement of the Estuarine Crocodile

3.1 Introduction

It is no question that all species must navigate an environment that encompasses conspecifics irrespective of their level of sociability. Spatial exclusion between individuals may occur to reduce competition and hostile behavior (Galezo *et al.*, 2017). On the other hand, some individuals make attempts to capitalize on shared spatial zones with conspecifics to find resources and avoid predation (Peignier *et al.*, 2019). These individuals may further alleviate possible social conflict by either associating with or evading specific conspecifics which eventually form the social hierarchy of the population (Robitaille *et al.*, 2021). Such patterns in a spatial organization form the spatial structure of most animal populations which is the basis on which social behaviors such as mating and care structures form and evolve (Kappeler, 2019).

The dynamics and spatial distribution of resources and conspecifics due to temporal changes is influenced by animal dispersal, predation, an individual’s reproductive state, seasonal changes in resource availability etc. Furthermore, as individuals grow and reach sexual maturity, the relationship between conspecifics changes as individuals learn to navigate interactions with other conspecifics. Essentially, the demographic structure of populations constantly experiences change as new social ties form and old ones die. An understanding of these dynamic patterns has a direct application to the population management of certain species (Banks & Lindenmayer, 2014). These dynamic patterns highlight the importance of spatial ecology, a field that examines how spatial distribution, resource availability, and interactions among individuals influence population dynamics and ecosystem processes.

Spatial ecology is the study of how organisms are distributed in space and how these spatial patterns influence and are influenced by ecological processes, interactions, and the environment (Ritchie, 2010). It integrates the movement, behavior, and interactions of individuals or populations with their habitats, considering factors such as resource availability, competition, predation, and environmental changes. Understanding spatial ecology is crucial because it provides insights into population dynamics, habitat use, resource partitioning, and how environmental changes affect ecosystems. For instance, spatial ecology is essential for conservation as it identifies critical habitats, migratory corridors, and strategies to mitigate human-wildlife conflicts (Kareiva *et al.*, 2011).

The importance of spatial ecology also lies in its ability to reveal how animals navigate their environments to meet biological needs, such as finding food, reproducing, and avoiding predators. It helps us understand the spatial structure of populations, including how individuals distribute themselves in relation to conspecifics and resources. This understanding is particularly significant for mobile or territorial species, where spatial interactions affect individual fitness, population viability, and ecosystem health. Studies by Nathan *et al.* (2008) have highlighted how spatial ecology can inform conservation by identifying areas of ecological importance, such as breeding sites or migratory corridors, to guide the implementation of protected areas.

Spatial ecology also introduces the concept of scale, examining how ecological patterns and processes vary across spatial and temporal dimensions. Ecologists recognize that ecological processes operate at multiple spatial scales, from local to global. For example, a study on small mammals' foraging behaviour emphasized how animals navigated fragmented landscapes, relying on sensory and social cues to select habitats. The study shows that as spatial scale increases from local foraging sites to broader habitat patches, animals face greater uncertainty and risk in habitat selection (Lima & Zolner, 1996). Another study on ungulate migration reveals how semi-permeable barriers, such as roads and development areas, alter migration patterns by modifying movement rates, detouring animals, and reducing the use of essential stopover habitats, thus impacting the functionality of migration routes. This demonstrates that spatial scale, from individual animal movement to population-level migration corridors, is crucial for understanding landscape connectivity (Sawyer *et al.*, 2012).

Spatial ecology also emphasizes the importance of landscape structure in shaping ecological processes. Landscape ecology, a sub-discipline of spatial ecology, focuses on the effects of landscape composition and configuration on ecological dynamics. For instance, the fragmentation of forests can alter species movement patterns, reduce genetic diversity, and increase the risk of extinction for certain species (Hanski, 1999). A study by Fahrig (2003) demonstrated that habitat fragmentation in forest ecosystems reduced connectivity, leading to a decline in species' ability to move between habitat patches, which can result in smaller population sizes and reduced genetic diversity. Such fragmentation increases the risk of local extinctions, especially for species with limited dispersal abilities.

Wildlife commonly utilizes restricted or confined spaces in which they move and travel. The location and size of this space is called the home range. It is an indication of an animal's behavioural repertoire as it searches to obtain food, shelter, and mates (Burt, 1943). Social conditions and anthropogenic factors, such as habitat fragmentation and human-induced changes, have a strong influence on home range for many wildlife species, and consequently affect the abundance and distribution of a population (Harris *et al.*, 1990). Therefore, understanding the dynamics of a species' movement, home range, and territoriality is vital for the effective conservation and management of any wildlife population (Hengeveld, 1993). More importantly, it is essential to understand the spatial requirements and hierarchical status of top predators because of their impact on animals in lower trophic levels, which can alter ecosystem structure and function (Terborgh *et al.*, 2001).

Spatial ecology is a crucial aspect of understanding crocodilian behaviour and conservation, providing insights into the ecological roles and survival strategies of these apex predators. Crocodilians, comprising species like alligators, caimans, gharials, and true crocodiles, inhabit a range of ecosystems from freshwater rivers and lakes to brackish waters and coastal regions. The study of their spatial ecology not only enhances our knowledge of their natural history but also informs conservation strategies in the face of habitat loss, climate change, and human-wildlife conflict.

Crocodiles, such as the Nile crocodile, *Crocodylus niloticus* in Africa, exhibit complex spatial behaviour influenced by environmental factors and social structures. Studies in the Okavango Delta have shown that Nile crocodiles use specific home ranges and engage in seasonal migrations linked to water levels and prey availability (Calvelrey & Downs, 2015). These patterns are critical for understanding how environmental changes, such as droughts or floods, impact their survival and reproduction. In America, the American crocodile, *Crocodylus acutus* demonstrates unique spatial ecology due to its coastal habitat preferences. Studies in coastal Mexico has highlighted the importance of mangrove forests and estuaries for their nesting and foraging activities (Rodriguez *et al.*, 2013). These habitats are under threat from coastal development and pollution, making spatial studies vital for developing effective conservation measures.

The critically endangered gharial, *Gavialis gangeticus* of the Indian subcontinent provides another example of the importance of spatial ecology in crocodilian conservation. Gharials primarily inhabit large river systems, and their spatial requirements include deep, fast-flowing waters and sandy banks for nesting. Studies in the Chambal River have documented their movement patterns and habitat use, emphasizing the need for riverine ecosystem protection to ensure their survival (Whitaker & Basu, 1983). The study of spatial ecology also extends to the smaller, lesser-known species like the dwarf crocodile, *Osteolaemus tetraspis* in West Africa. Research on their habitat use in Gabonese forests has shown that they prefer isolated, undisturbed water bodies, which are increasingly threatened by logging and agriculture (Eaton, 2010).

Although generally described as solitary animals, crocodilians exhibit substantial interspecific discrepancy in their social skills. The American alligator, *Alligator mississippiensis* for example form large-scale breeding and basking aggregations while the estuarine crocodile seem to display intolerance towards conspecifics (Lang, 1987).

The estuarine crocodile is the apex-predator in its ecosystem and feeds on a variety of prey animals. It is also the most widespread crocodilian with an extensive distribution range, occurring in coastal areas, estuaries, rivers, inland swamps, and off-shore islands (Brien *et al.*, 2008) suggesting a capability for travelling long distances. In Sabah, populations grew considerably since the implementation of protection in 1982 (Webb *et al.*, 2010). Forty years later, the results of the demographic study from the present study (chapter 3) confirm a stable, but possibly still recovering population. Although the densities vary significantly from one river system to another, a large growth or depletion in the population is expected to change the dynamics of the broader community and environment (McCanns *et al.*, 2005).

Recent telemetry studies have challenged the previously held belief that *C. porosus* are exclusively territorial, with dominant males excluding conspecifics from their home ranges. For instance, research by Campbell *et al.* (2013) observed that large adult male *C. porosus* often inhabit areas in close proximity to each other, suggesting a more complex social structure than previously understood. Similarly, Read *et al.* (2007) reported that translocated male *C. porosus* exhibited strong site fidelity and remarkable navigational skills, returning to their original capture sites after being moved significant distances. These findings indicate that *C.*

porosus may not be strictly territorial and that their social interactions and spatial behaviours are more intricate than earlier assumptions.

This species holds the title of the world's largest living reptile, with geographic distributions spanning from eastern India through Southeast Asia to northern Australia. Notably, these crocodiles are responsible for a large number of unprovoked fatal attacks on humans annually, highlighting their status as one of the most dangerous crocodilian species (Fukuda *et al.*, 2015; Britannica, 2024). Handling problem crocodiles by translocating them to remote areas is a questionable solution simply because many of them are found to return to their capture sites (Walsh & Whitehead, 1993). Homing information on translocated crocodilians has been obtained mainly by surveillance at the original capture site indicating that these individuals are likely to exhibit site dependencies.

Marking individuals to enable mark-translocate-recapture methods is a good and cheap method to identify returning individuals, however, it lacks information about the journey of returning individuals, or the timeline of the journey. For this, telemetry in required. For instance, GPS telemetry has been instrumental in understanding the spatial dynamics of the Morelet's crocodile, *Crocodylus moreletii* in Belize, providing insights into their responses to seasonal changes and human disturbances (Platt *et al.*, 2009). Besides that, spatial data on the Siamese crocodile, *Crocodylus siamensis* in Southeast Asia has guided the establishment of protected areas and informed reintroduction programs aimed at boosting their dwindling populations (Simpson *et al.*, 2006).

Numerous efforts in monitoring translocated crocodilians by radiotelemetry have been made over short distances and short timelines (Kay, 2004). Studying intricate movement patterns in crocodilians by conservative radiotelemetry is however difficult due to several reasons such as their cryptic behaviour, they have an extensive geographic range, they live in isolated areas and they are easily disturbed by human presence. On the contrary, satellite tracking permits fundamental and continuous data collection from animals located in remote areas and over larger spatial and temporal scales. Furthermore, this method does not require human interference as opposed to manual tracking.

Human-crocodile conflict is an escalating issue in many parts of the world, particularly in regions where human populations encroach upon crocodile habitats. In Sarawak, statistics reveal that from 1941 to 2013, a total of 118 crocodile attacks were reported, with 64 being fatal (Lading, 2013). This averages 1.66 attacks per year. However, more recent data from the Sarawak Forestry Corporation (SFC) indicates an increase in crocodile-related incidents. Between 2020 and 2024, the Bintulu division alone recorded 108 crocodile attacks, averaging 21.6 attacks per year (Borneo Post Online, 2024).

The conflict arises from the overlapping spatial requirements of humans and crocodiles, leading to dangerous encounters that can result in injury or death for both humans and crocodiles (Aust *et al*., 2009; Pooley, 2016). As human activities increasingly infringe upon natural habitats, understanding the spatial ecology of crocodiles becomes critical for developing effective strategies to mitigate these conflicts (Walsh & Whitehead, 1993; Fukuda *et al*., 2014).

For example, in Australia, where human-saltwater crocodile conflicts are common, tagging studies have revealed that saltwater crocodiles can travel significant distances along coastlines and rivers. Studies have recorded average daily movement distances of up to 3.5 km per day and maximum recorded movements exceeding 900 km over several months (Campbell *et al.*, 2013; Read *et al*., 2007). Understanding these patterns has allowed wildlife managers to anticipate potential conflict zones, particularly during the breeding season when crocodiles are more likely to move into areas frequented by humans. By identifying these high-risk areas, authorities can issue warnings, implement safety measures, and relocate problem animals to reduce the likelihood of attacks (Fukuda *et al.*, 2014).

In Sabah, the human-crocodile conflict has intensified in recent years, notably along the Kinabatangan River and extending to other rivers and coastal regions. The escalation of human activities such as fishing, agriculture, and ecotourism has led to more frequent and often fatal encounters between humans and crocodiles. Factors contributing to this increase include habitat loss and a decline in large prey, compelling crocodiles to venture closer to human settlements in search of food (The Borneo Post, 2022).

Factors contributing to this increase include habitat loss and a decline in large prey, compelling crocodiles to venture closer to human settlements in search of food. Additionally, human encroachment into crocodile habitats has exacerbated these conflicts, as development projects and land-use changes disrupt the natural environments of these reptiles (The Vibes, 2023).

Previous GPS tracking of crocodiles in the Kinabatangan River has revealed that these animals tend to use specific stretches of the river for hunting and nesting, which often overlap with human fishing zones (Evans, 2016). Identifying these critical areas, are important for wildlife managers to establish no-fishing zones, especially during peak nesting seasons, to reduce the likelihood of encounters.

Furthermore, spatial ecology studies have highlighted the importance of maintaining intact riparian habitats along the riverbanks, which provide essential cover and nesting sites for crocodiles (Fukuda *et al*., 2014; Aust *et al*., 2009). When these areas are destroyed, crocodiles are more likely to venture into areas used by people, increasing the likelihood of human-crocodile conflicts (Pooley, 2016). Protecting these habitats serves as a key strategy for reducing such conflicts. In addition, data from tagging studies have shown how spatial information can help inform the placement of warning signs, the timing of community awareness campaigns, and the development of rapid response protocols for when crocodiles are spotted near human settlements (Read *et al*., 2007).

Primary objective

To understand the spatial ecology of *C. porosus* in Sabah to inform effective strategies for mitigating human-crocodile conflicts in the region.

Secondary objectives

1. To determine movement patterns of adult *C. porosus* in Sabah.
2. To determine key habitats used by *C. porosus* in Sabah.
3. To assess how man-made structures, in particular the bridge across the Kinabatangan River, and human activities, such as agriculture, tourism, and urban development, influence crocodile movements and habitat use.

3.2 Methodology

3.2.1 Sampling Site

The Kinabatangan River, located on the east coast of Sabah is the second longest river in Borneo and the longest river in Sabah, with an approximate length of 560 km (Boonratana, 2000). The area surrounding the Kinabatangan River consists of several habitat structures including riparian forests, swamp forests, dipterocarp forests and seasonally flooding forests (Estes *et al.*, 2012). These forests are surrounded by oil palm plantations that have led to an expansion of human presence on the river (Ancrenaz *et al.*, 2004). The Kinabatangan floodplain is renowned for its rich biodiversity, encompassing a wide array of species across various taxa. This unique ecosystem supports approximately 60 mammal species, including significant populations of the Asian elephant (*Elephas maximus*) and the proboscis monkey (*Nasalis larvatus*). Avian diversity is also remarkable, with nearly 200 bird species recorded, among them eight species of hornbills and the endangered Storm's stork (*Ciconia stormi*). Herpetofauna are well-represented, with 27 species of reptiles and amphibians documented. Additionally, the floodplain's freshwater systems harbour over 100 fish species, highlighting the area's ecological significance (Birdlife International, 2003).

The Lower Kinabatangan Wildlife Sanctuary (LKWS) (N5.415787; E118.034383), located on the Kinabatangan River was established in 2005 (Figure 3.1). It consists of 10 lots separated by oil palm plantations and other types of land use. The river is home to a robust population of *C. porosus* which has numerically recovered from an endangered status at the time protection was started in 1982. Capture sites were spread across approximately 10 kilometres of river length. As well as being easily accessible due to the proximity of the Danau Girang Field Centre (DGFC), this river stretch was chosen for trapping because of its high abundance of large crocodiles compared with other sections of the river.

3.2.2 Sample Collection

All aspects of the tagging process, including the satellite tags and the protocols for capture, attachment, and release, were consistent with those used by the previous PhD student, Luke Evans. This ensured methodological continuity and comparability between studies.

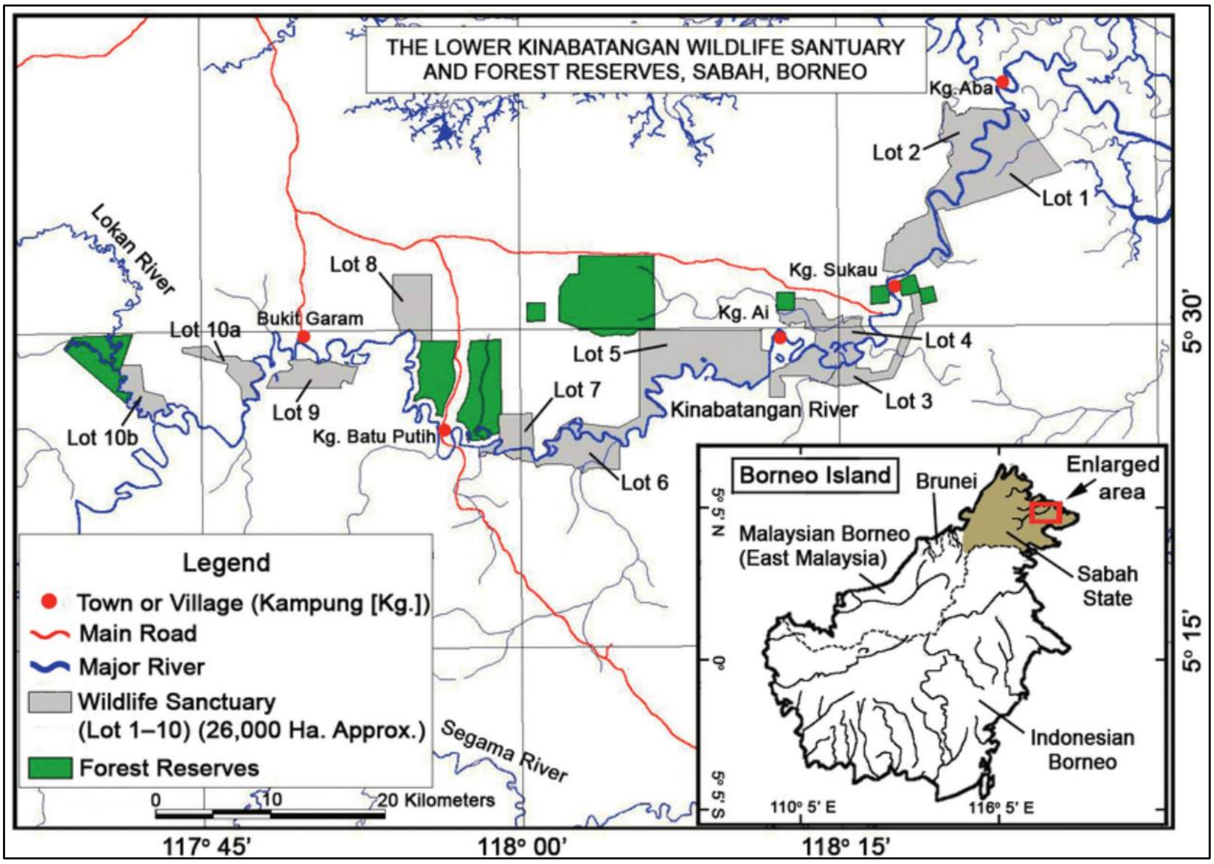


Figure 3.1. Lower Kinabatangan Wildlife Sanctuary (Van de Water, 2013).

Over a three-year period from 2017 to 2019, satellite tags were deployed on crocodiles within the LKWS. These tags were sourced from African Wildlife Tracking (AWT) located in Rietondale, Pretoria, South Africa. The AWT units utilize the Iridium satellite constellation, which not only provides location fixes but also allows for two-way communication. This capability enables researchers to send commands to the tags after they have been attached to the monitored crocodiles. The collected data is uploaded directly to a secure central server, where it is made accessible in both .xls (Excel) and .kml (Google Earth) formats. Tagging procedures were conducted under strict ethical guidelines to ensure minimal stress and harm to the animals, following approved protocols and permits issued by the relevant authorities.

To ensure the tags were appropriate for the animals, all devices conformed to scientifically-approved standards, with the weight of each tag kept between 400-850 grams, representing less than 1% of the crocodile's total body weight (Tuyttens *et al.*, 2002; Theuerkauf *et al.*, 2007). To minimize any potential impact on the crocodiles, the tags were crafted from reinforced moulded plastic and designed with a streamlined shape to reduce drag while moving through the water.

Crocodiles were captured using a portable steel mesh trap measuring 4 x 1.5 x 1 meters in dimension. The trap was constructed with a lightweight steel frame and meshing, allowing it to be easily transported between capture sites. The trap was equipped with a straightforward trigger mechanism: a rope-based system where the bait, typically chicken intestines, was secured at the back of the trap. When the crocodile bit the bait, the tension would release the door latch, capturing the animal. Traps that emitted a strong bait odour, and were positioned either just above or slightly in contact with the water's surface, proved to be the most effective.

After successfully trapping an individual, it was transported to a suitable area where the handling and tagging process could be conducted safely and efficiently. Before opening the trap door, at least two jaw ropes were secured around the crocodile's jaws. A noose was carefully threaded over the jaws using a stick, and a rag was placed over the animal's eyes to minimize stress and reduce the likelihood of aggressive movements. The two top jaw ropes were kept under tension as the trap door was opened, maintaining control over the crocodile's movements.

At this point, the crocodile may engage in a "death roll," a 360° lateral spin typically used for subduing prey. While this behaviour can be intense, it also tires the animal, making the subsequent handling easier. Once the crocodile had calmed down, its jaws were securely bound using strong tape on top of the rope. A capture team, with one person assigned for every meter of the crocodile's length, restrained the animal while the jaws were secured, and the blindfold was correctly repositioned. For larger crocodiles, the legs were also tied to prevent further death rolling and other violent movements.

Morphometric measurements were recorded, and the sex of the crocodile was determined. The satellite tag was then attached to the nuchal plate, a region bordered by six scutes along the crocodile's back. To secure the tag, holes were drilled through the four central scutes, and plastic-coated steel wire was threaded through both the holes and the tag. These wires were then fastened securely at the top of the tag using clamps. Additionally, wire was threaded sub-dermally beneath the nuchal plate to provide a secondary attachment, which is crucial for ensuring the tag remains in place long-term. To further secure the tag, the base was coated with a quick-drying epoxy resin. Before releasing the crocodile, it was carefully repositioned to face the river. The legs were untied while ensuring they remained suspended above the ground, and the mouth restraints were then removed. Finally, the blindfold was taken off, prompting the crocodile's instinctive behaviour to enter the water. The tag began transmitting data immediately upon release.

3.2.3 Statistical analysis

Habitat use analyses were performed using R version 4.3.1, with Minimum Convex Polygons (MCP) and Kernel Utilization Densities (KUD) constructed through the 'adehabitatHR' and 'PBSmapping' packages, and spatial visualizations were further refined in QGIS version 3.36. MCP was employed to define the total home range for each individual crocodile, while KUD provided estimates for the core (50%) home range, where an individual spends the majority of its time, and total (90%) home range, encompassing a broader area used by an individual for activities like foraging/exploring. home ranges. The kernel smoothing parameter (h) was adjusted based on individual movement patterns, and all home range polygons were exported as shapefiles for visualization and mapping in QGIS. The KUD values were expressed in square meters and converted to square kilometers for reporting. Unless otherwise noted, all means are expressed as the mean (± s.d.).

To quantify individual movement patterns, daily and weekly movement metrics were calculated using R, with the 'geosphere' package applied to calculate distances between consecutive GPS points based on the haversine formula. Daily mean movement distances were computed by summing the total distance covered each day for each individual, while weekly movements were derived by aggregating the daily movements over each seven-day period. These movements were visualized in R using the 'ggplot2' package to create bar charts.

Distance to centroid analysis was conducted to evaluate movement patterns relative to the geometric center of each individual's home range. This was accomplished in R by calculating the Euclidean distance between each GPS point and the centroid of the home range polygons (both MCP and KUD).

To address the hypothesis that crocodiles avoid crossing under man-made structures, movement points were plotted in QGIS relative to the location of a significant bridge across the Kinabatangan River. GPS points of individuals that were tagged on each side of the bridge was plotted to test whether individuals showed avoidance or moved freely across this anthropogenic barrier. All spatial analyses were carried out using R and QGIS, with plots and maps generated to explore habitat use, movement ecology, and the potential influence of anthropogenic factors on the behavior of saltwater crocodiles in the Kinabatangan River system.

3.3 Results

Over the course of this study, six crocodiles were successfully captured. Of these, two were deemed undersized for tagging and were promptly released after measurements and DNA samples were collected, in compliance with ethical guidelines. Among the remaining four individuals that were tagged, equipment failure occurred in two cases immediately upon release, resulting in the loss of data. Consequently, the study was left with usable data from only two tagged crocodiles. To enhance the sample size, data from seven crocodiles tagged during the previous work of PhD student, Luke Evans were incorporated into this study, bringing the total sample size to nine individuals (Table 3.1) The capture location of each individual is shown in Figure 3.2.

Table 3.1. Morphometric measurements (cm) for each individual sampled.

ID	SEX	TOTAL LENGTH (CM)	SV LENGTH (CM)	HEAD LENGTH (CM)	Origin	Tagging Status
F1	F	396.0	182.3	96.0	Evans, 2016	Successful
F2	F	313.0	156.0	63.0	Evans, 2016	Successful
F3	F	331.0	162.0	67.5	Present study	Successful
F4	F	333.5	155.0	65.0	Present study	Successful
M1	M	403.0	190.6	82.0	Evans, 2016	Successful
M2	M	377.0	174.0	75.0	Evans, 2016	Successful
M3	M	518.0	234.0	114.0	Evans, 2016	Successful
M4	M	389.0	177.0	78.0	Evans, 2016	Successful
M5	M	356.0	162.0	69.7	Evans, 2016	Successful
M6	M	392.0	179.5	80.0	Present study	Battery failure
M7	M	355.0	160.5	67.0	Present study	Battery failure
KTT01	NA	245.0	112.0	49.5	Present study	Not suitable
KTT02	NA	187.0	88.0	39.5	Present study	Not suitable

Figure 3.2. Capture and tagging locations for all nine individuals. The yellow dots represent individuals tagged from the present study (F3 & F4) while the red dots represent individuals tagged by previous student, Luke Evans (F1, F2, M1 -M5).

The total distance travelled and average range of movement (ROM) of each individual was calculated from the GPS positions for each animal (Table 3.2). The longest distance travelled was by female F1 with a total distance of ~640 kilometers over a duration of 224 days, followed by male M4 with a distance of ~351 km, over 108 days. Female F2 and F4 travelled very short distances, covering ~37 km and ~51 km, over a duration of 39 and 15 days, respectively. On average, the females moved longer distances (249 ± 391.4 km, $p>0.05$) than males (219 ±132.0 km, $p<0.05$).

Table 3.2. Movement and home range metrics for females F1 -F4 and males M1 – M5.

ID	Total Distance Travelled (km)	Total Time Travelled (Days)	Average ROM (kmd^{-1})	Total Home Range Size (km^2)	Core Home Range (km^2)	Core to Total Ratio
F1	640.4	224	2.85	26.0	4.5	0.2
F2	37.2	39	0.98	1.7	0.2	0.1
F3	266.2	134	1.98	7.2	1.8	0.2
F4	51.8	15	3.45	5.4	1.5	0.3
Mean ± s.d	*249.0 ±391.40*	-	*2.32 ±1.08*	*10.08 ±10.86*	*1.93 ±1.67*	-
M1	160.0	52	3.07	1.4	0.4	0.3
M2	137.5	41	3.35	12.8	2.7	0.2
M3	179.5	71	2.52	4.6	1.1	0.2
M4	351.0	108	3.25	6.8	1.2	0.2
M5	268.6	28	9.59	41.7	9.2	0.2
Mean ± s.d	*219.0 ±132.00*	-	*4.36 ±2.94*	*13.46 ±16.33*	*2.48 ±3.61*	-

Home range sizes, both total and core, also varied among individuals. Male M5 had the largest total home range, covering 41.7 km², with a core home range of 9.2 km², resulting in a core-to-total ratio of 0.2. In contrast, individuals F2 and M1 had notably smaller total home ranges (1.7 km² and 1.4 km², respectively), but they displayed relatively high core-to-total ratios (0.3 each).

Figure 3.3 presents the mean daily movement of all individuals, comprising both male and female crocodiles. Male M5 indicated the most movement at ~9 ±2.32 km per day, while the least movement was ~1 km ±0.60 per day, by female F2.

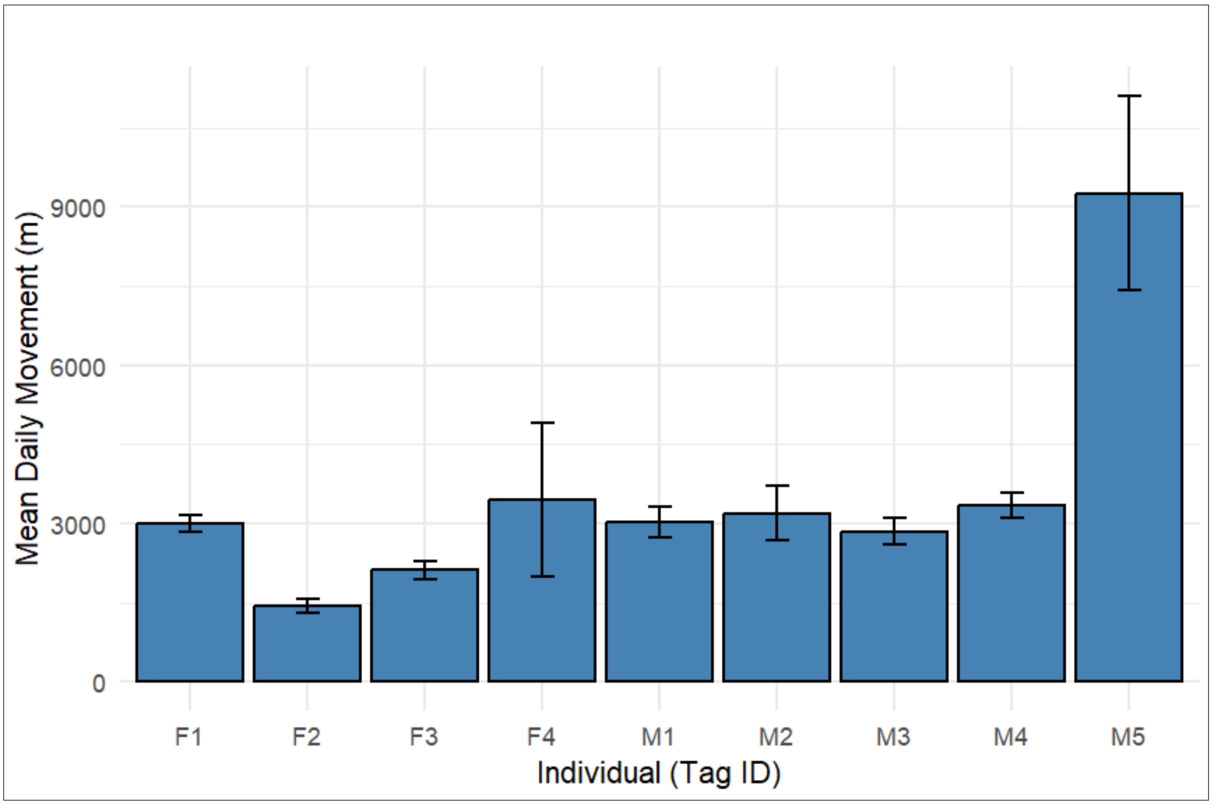


Figure 3.3. Mean daily movement (m) for nine tagged crocodiles (F1–F4: females, M1–M5: males). Bars represent the mean movement, and error bars indicate standard deviation.

The average daily movement of the remaining individuals ranged from 1.98 ±0.72 km per day to 9.59 ±1.17 km per day. Figure 3.4 illustrates the mean weekly movement of the tagged individuals. Male M5 shows the greatest movement, covering an average of 52.0 ±14 km per week, which far surpasses the movement patterns of the other individuals. Male M4 follows with a weekly movement of 21.0 ±3.0 km, making it the second most active individual in the group. Male M2 and female F1 also display relatively high weekly movements, with mean distances of about 19 ±6.0 km and 19 ±0.9 km, respectively.

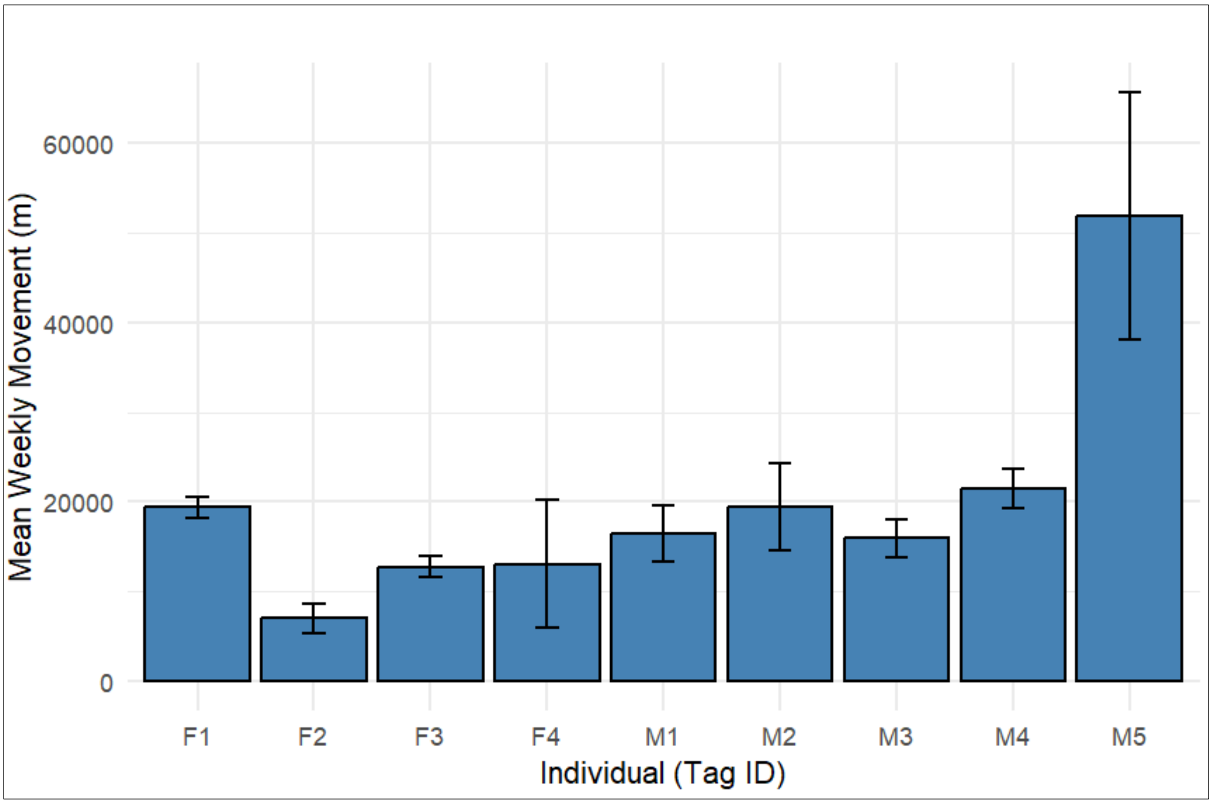


Figure 3.4. Mean weekly movement (m) for nine tagged crocodiles (F1–F4: females, M1–M5: males). Bars represent the mean movement, and error bars indicate standard deviation.

At the lower range, female F2 exhibited the smallest mean weekly movement, covering 7.0 ±1.4 km per week. The other individuals displayed moderate weekly movements: male M1 at 17.0 ±2.1 km per week, M3 at 16.0 ±1.9 km per week, female F3 at 13.0 ±1.7 km per week and F4 at 13.1 ±6.0 km per week.

Distance to Centroid

Figure 3.5 shows the distance to centroid for four female crocodiles that were tagged. Graph (a) shows the distance to the centroid for the individual F1 from March to August. There are several noticeable spikes, suggesting that this individual made substantial excursions away from its core area during specific periods, with the highest distance to the centroid reaching over four kilometres. This spike is concentrated around March and April, after which the movement stabilizes and the distances become less variable, as this individual spends a considerable amount of time close to its centroid, reflecting strong site fidelity.

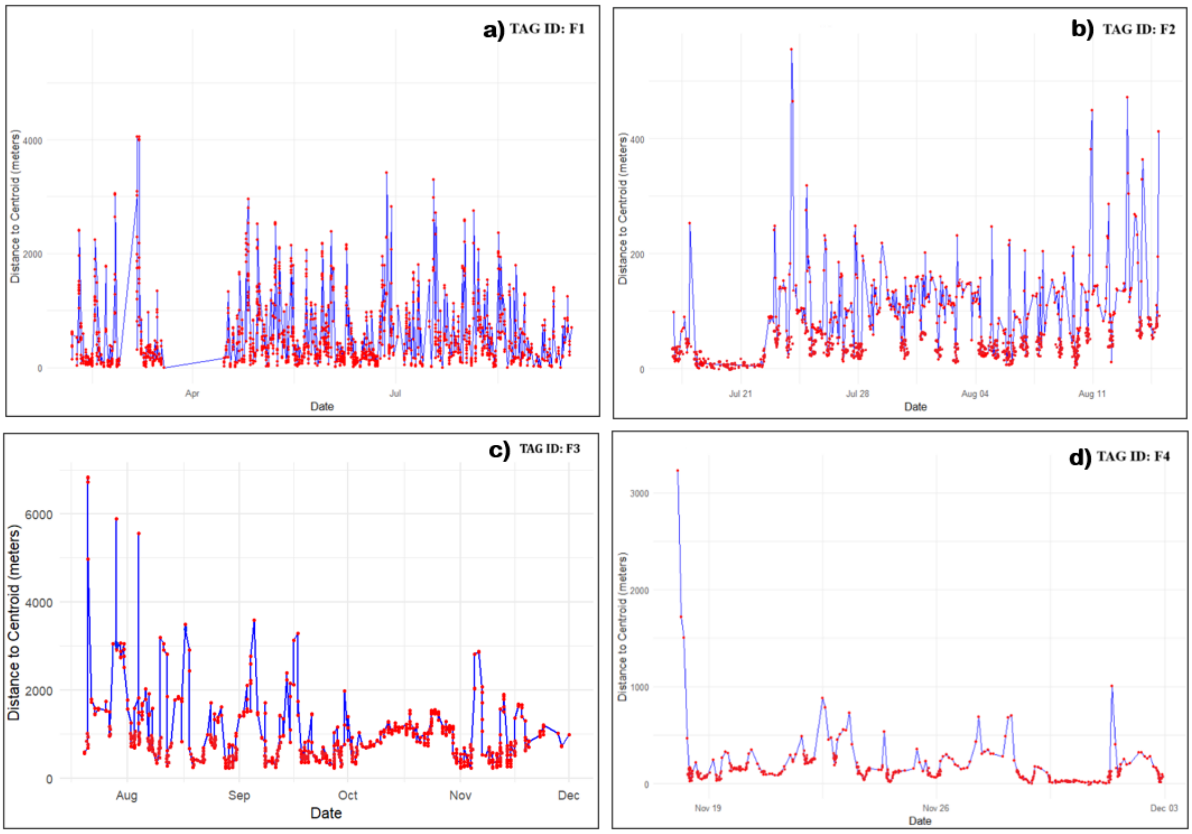


Figure 3.5. Distance to centroid (m) for females a) F1, b) F2, c) F3 and d) F4. Red dots show GPS locations, indicating the distance from the home range centroid. The blue line connects these points, illustrating changes in movement over time. Peaks in the blue line represent periods when the crocodile moved farther from the centroid.

Similar to F1, the distance to centroid for individual F2 (b) displays a series of fluctuations in distance. Throughout the observed time frame, F2 often maintained relatively low distances to the centroid, suggesting a tendency for site fidelity and a preference for remaining within a core area. However, several pronounced peaks are evident, particularly around late July and early August.

Individual F3 (c) showed notable variability in its movement patterns, particularly in July and August, where there were several prominent spikes in distance to the centroid, with the highest value surpassing six kilometres. After this period, F3's movements become more stable, with distances to the centroid generally staying under two kilometres for the remainder of the year, with occasional excursions. From September to December, F3 exhibits smaller and more recurrent fluctuations, suggesting a tendency towards site fidelity, as the movements are concentrated within a more confined area.

The movement pattern of individual F4 shows a sharp initial spike in distance to the centroid, reaching over three kilometres in mid-November (d). Following this, there is a marked reduction in movement, with most distances remaining below one kilometre for the rest of the tracking period. Although there are small fluctuations between 500 meters and one kilometre, F4 consistently stays within a close range of the centroid, suggesting strong site fidelity. All female individuals exhibited strong site fidelity, spending significant amounts of time close to their respective centroids, which indicates a preference for residing within core home ranges.

In contrast, the males exhibited noticeably different movement strategies (Figure 3.6). Individual M1 demonstrates a wide range of movement, with frequent shifts in its distance from the centroid, peaking several times throughout the observation period (a). The distance to centroid fluctuates consistently between zero and 1.5 km, showing multiple spikes in movement. The consistent variation in distance suggests that this individual exhibit strong nomadic behaviour, as it does not remain near its centroid for extended periods.

Individual M2's movement pattern shows a relatively low and consistent distance from the centroid during early February, with small fluctuations typically staying below 500 meters. From mid-February, there is a notable increase in variability, with peaks exceeding one kilometre, and a significant spike in early March reaching over three kilometres. These large shifts suggest that M2 does not exhibit strong site fidelity, especially later in the tracking period, where its movement pattern becomes more irregular and expansive, indicating more exploratory or nomadic behaviour.

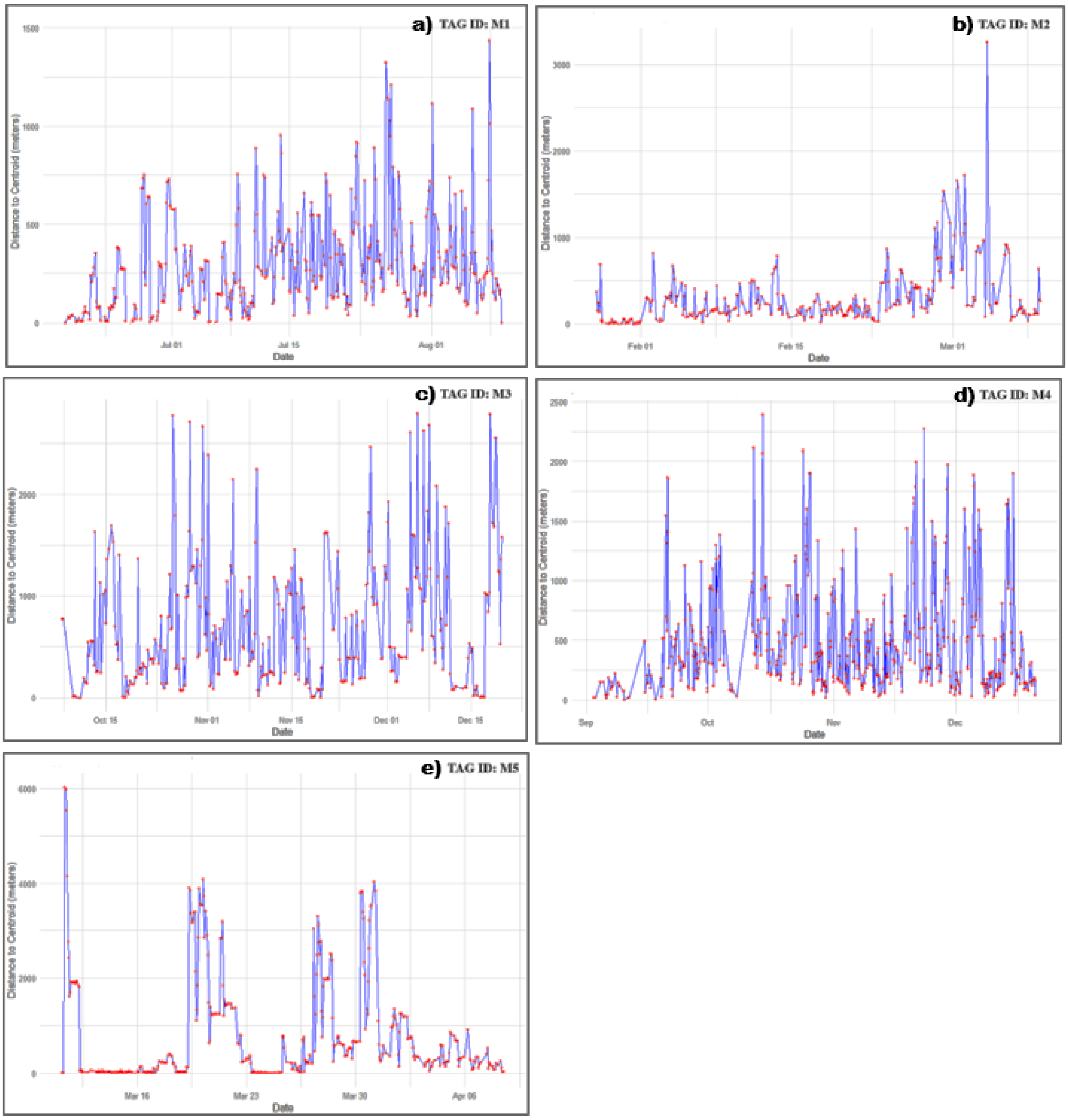


Figure 3.6 Distance to centroid (m) for males a) M1, b) M2, c) M3, d) M4 and e) M5. Red dots show GPS locations, indicating the distance from the home range centroid. The blue line connects these points, illustrating changes in movement over time. Peaks in the blue line represent periods when the crocodile moved farther from the centroid.

Individuals M3 (c) and M4 (d) show similar movement patterns to individual M1, but at different magnitudes. The graphs show frequent and substantial fluctuations in the distance from the centroid throughout the observed periods. Both graphs highlight frequent peaks exceeding one kilometre, with several peaks surpassing two kilometres, indicating the lack of consistent site fidelity. There are no clear long-term periods of centricity exhibited by individual M3.

Individual M5 exhibits a distinctive movement pattern that is quite different from the other males, indicating a more nomadic behaviour. The graph shows significant fluctuations in distance from the centroid, with a sharp spike at around six kilometres in early March and multiple peaks of around four kilometres. However, these long-distance movements are interspersed with periods of much shorter distances to the centroid, where M5 appears to stay closer to the centroid.

Home Range

Following the analysis of the distance to core areas, the Kernel Utilization Distribution (KUD) provided more detailed view of the spatial structure of home ranges, highlighting the core and broader areas used by the tagged individuals (Figure 3.7). For female F1, the 50% core home range is concentrated in the winding stretch of the river within Lot 7, extending slightly into Lot 6 of the Kinabatangan River (Figure 3.7a). This area is highly clustered with movement points, indicating frequent usage. The 90% total home range spans a larger area, stretching into the Pin-Supu Forest Reserve, with the furthest movements occurring towards the north, away from the main river and closer to the forested areas.

Female F3's 50% core home range is tightly clustered within Lot 6 of the Kinabatangan River, showing a distinct, concentrated use of a small area along the river (Figure 3.7c). The 90% home range extends outward, covering a much larger area that includes the river but also stretches into the adjacent unprotected forest areas. The spread of the home range suggests frequent returns to the core area with occasional longer movements within this broader range.

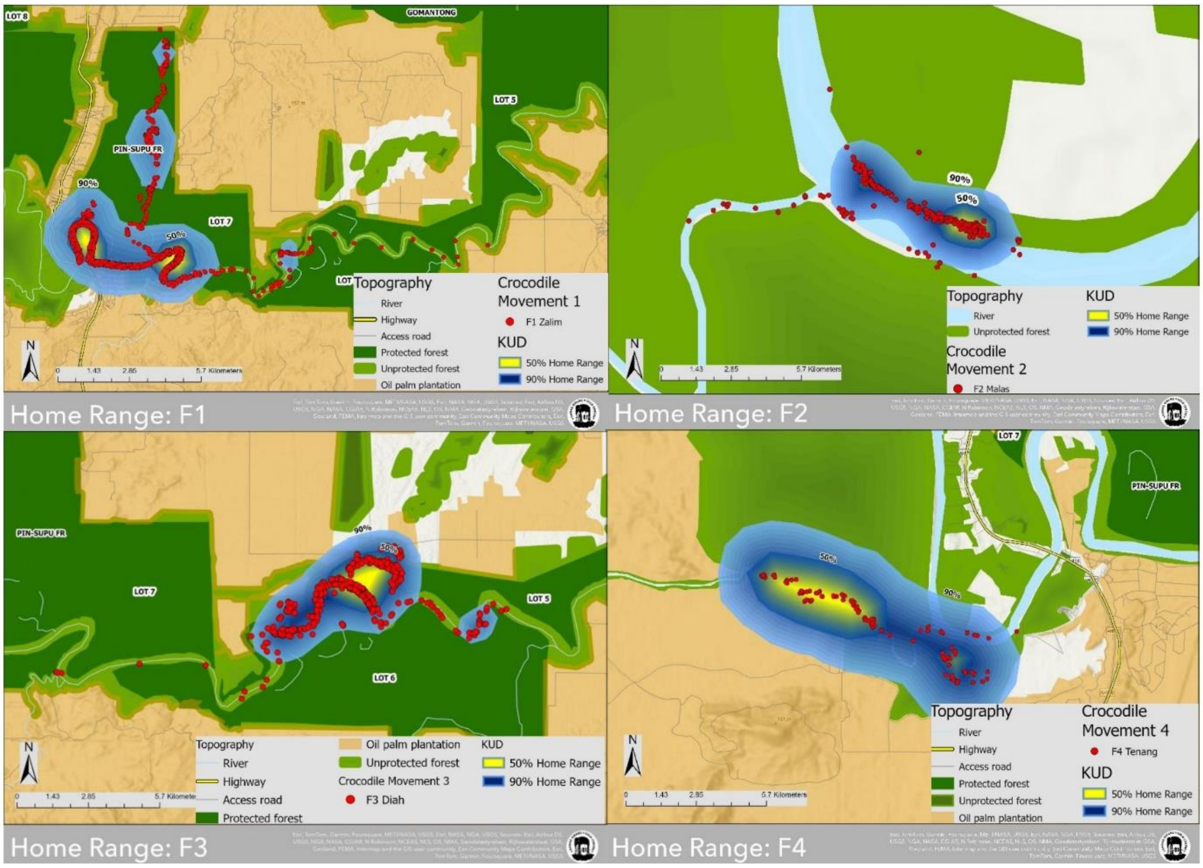


Figure 3.7. Kernel Utilization Distribution (KUD) 50% (core) and 90% (total) Home Ranges for females a) F1, b) F2, C) F3 and d) F4. Red dots show GPS locations. Blue shapes represent the 50% core home range, and yellow shapes represent the 90% total home range.

Female F4 shows a 50% core home range that is centered in a straight stretch of the river, just downstream of Lot 7 of the Kinabatangan River (Figure 3.7d). The movements are tightly concentrated along this stretch of the river, indicating consistent use of this narrow area. The 90% home range extends downstream but remains relatively localized, showing less extensive movement compared to the other females. For female F2, the 50% core home range is confined to a small, curved portion of the river, indicating consistent use of this specific area (Figure 3.7b). The 90% home range extends along the river, but in a much narrower fashion compared to the other individuals, suggesting F2's movements are largely confined within this smaller section of the river. The range remains within the riverine corridor, without extending into the adjacent forested or plantation areas.

The home ranges of the five male crocodiles, as illustrated by their KUD 50% and 90% estimates, exhibit prominent variability in size and distribution (Figure 3.8). Each male crocodile occupies a distinct section of the river, with some showing concentrated core areas of activity while others spread their movements more widely across the landscape.

The home range of male M1 is concentrated primarily within Lot 5 and Lot 6 of the study area (Figure 3.8a). The 50% KUD, representing the core home range, is clustered around a bend in the river, indicating high usage of this specific section. The 90% KUD extends further along the river but remains confined to the same general area, showing that M1's movements are comparatively localized.

M2's home range is characterized by two distinct clusters of activity within the 90% KUD (Figure 3.8b). The first area is situated in Lot 6, where both the 50% and 90% KUD are concentrated, indicating this is where M2 spent most of its time. The second cluster of the 90% KUD is located along the river to the west, near the bend in the river, but separate from the main home range. This indicates concentrated movement in these two specific areas rather than having a continuous home range.

M3's home range consists of two distinct 50% KUD areas, both located within Lot 6 of the Kinabatangan River (Figure 3.8c). These two high-use zones are connected by a continuous 90% KUD that stretches along the river, forming an elongated home range. The presence of two separate core areas indicates that M3 regularly moves between these two critical sections along the river. The northern core area shows the highest density of use, while the southern section also represents an important area of activity. The entire home range is confined within Lot 6, with no indication of movement beyond this area.

The home range for male M4 is concentrated along a linear stretch of the river, primarily within Lot 6, with the 50% KUD located in the eastern part of the range (Figure 3.8d). The 90% KUD extends westward, reaching into Lot 7, covering a wider area along the riverbanks but still maintaining a linear pattern of movement. There is no sign of movement beyond the river's path, and the concentration of core activity is focused along the boundary between Lots 6 and 7 in the Kinabatangan River.

M5's home range consists of two distinct 50% KUD sections, both located within the 90% KUD. The first 50% KUD area is positioned in Lot 6, suggesting concentrated movement in this portion of the river (Figure 3.8e). The second 50% KUD area, farther east, extending into Lot 5, indicates a much higher movement concentration than the first one. This pattern indicates movement between these two core areas, with M5 utilizing both regions frequently.

The 90% KUD spans a significant length of the river, connecting the two 50% KUD sections and covering a large linear stretch from Lot 6 to Lot 5 of the Kinabatangan River.

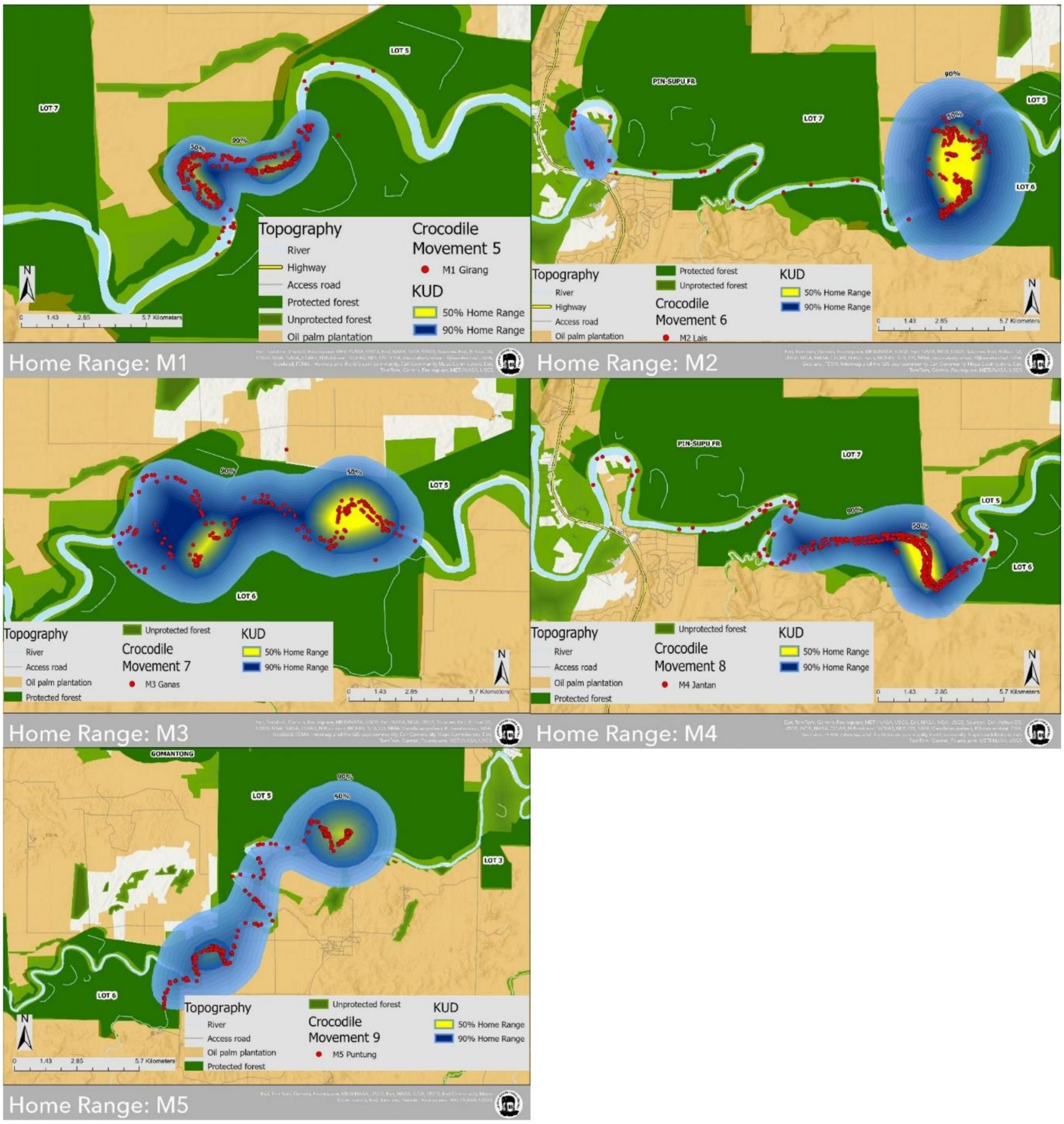


Figure 3.8. Kernel Utilization Distribution (KUD) 50% (core) and 90% (total) Home Ranges for males a) M1, b) M2, C) M3, d) M4 and e) M5. Red dots show GPS locations. Blue shapes represent the 50% core home range, and yellow shapes represent the 90% total home range.

Movement patterns of individuals in relation to the man-made bridge that spans over the Kinabatangan River were also characterised. All nine tagged individuals showed no evidence of crossing under the bridge. Five individuals in particular as shown in Figure 3.9 - 3.13, demonstrate clear patterns of movement that suggest avoidance of the man-made bridge.

The movement points, represented as clusters of red dots, show each individual approaching the bridge but not passing underneath it.

For several individuals, dense clustering was exhibited just short of the bridge. This is most evident in F1, F4 an M2 where the individuals travel close to the bridge from various directions, but their paths turn back upon reaching the bridge structure. Individual F1 spent the majority of its time within the 10 km stretch downriver of the bridge. Despite frequent clustering of points in the area just after the bridge (Figure 3.9), it never crossed under it, even though it came within 20 meters of it on several occasions. Individuals F2 (Figure 3.10) and M2 (Figure 3.11) showed similar patterns, although there was no high-density clustering right before the bridge as exhibited by Individual F1. Individual F2 repeatedly moved along the river's curve near the bridge, yet even with a fair distance to the crossing point, there is no indication of it proceeding under the bridge (Figure 3.12). Individual M4 similarly highlights this avoidance behavior (Figure 3.13).

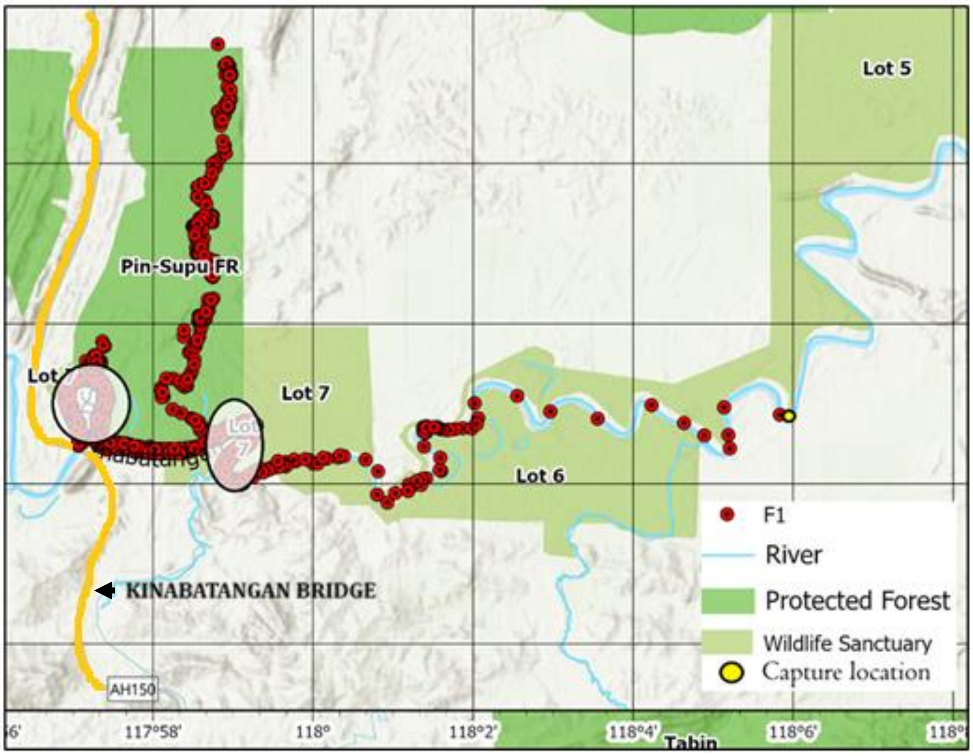


Figure 3.9. Movement of female F1 relative to the man-made bridge over the Kinabatangan River. The grey line represents the bridge, the red dots represent GPS points, the yellow dot represents capture & tagging location, the faded white circles represent core 50% home ranges.

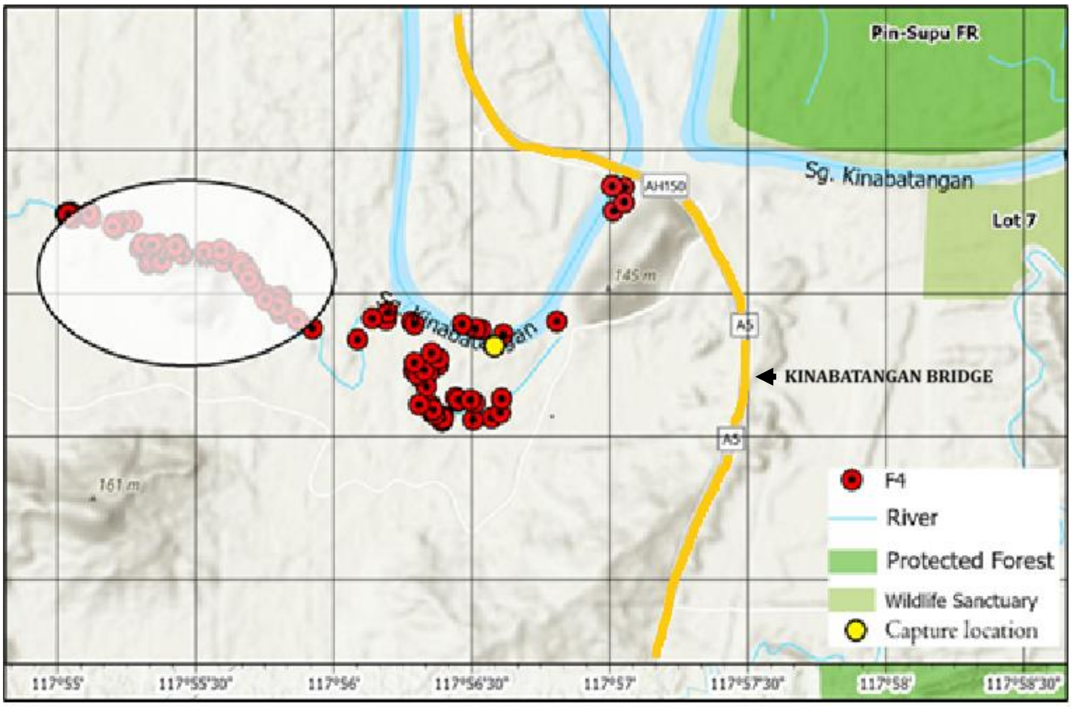


Figure 3.10. Movement of female F4 relative to the man-made bridge over the Kinabatangan River. The grey line represents the bridge, the red dots represent GPS points, the yellow dot represents capture & tagging location, the faded white circles represent core 50% home ranges.

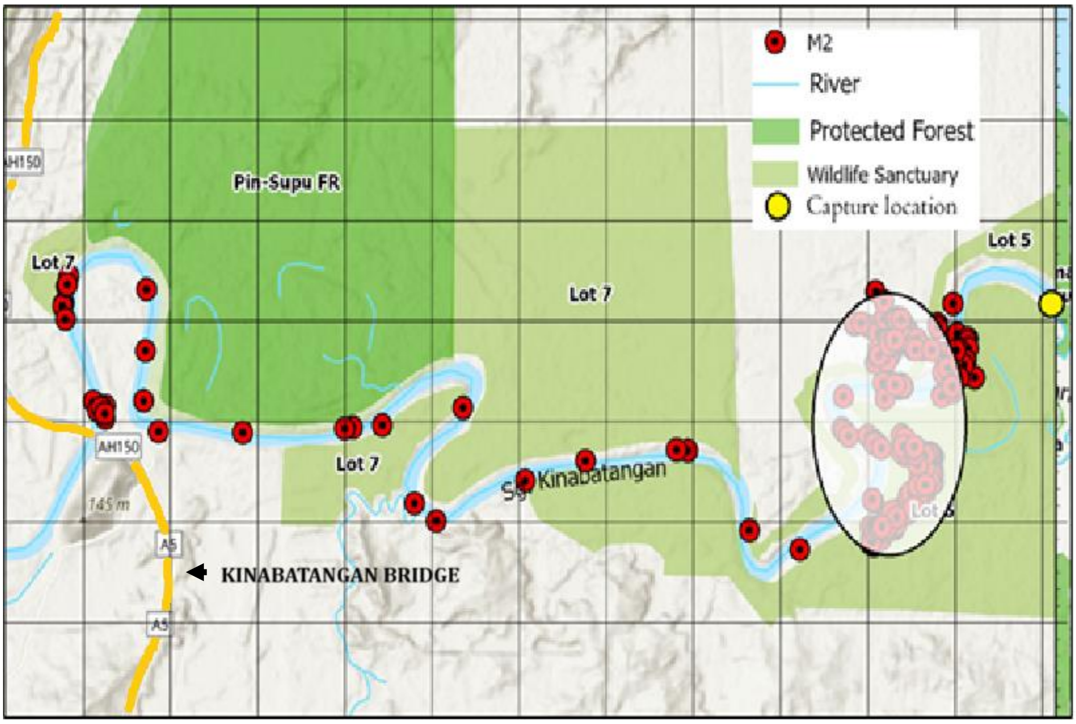


Figure 3.11. Movement of male M2 relative to the man-made bridge over the Kinabatangan River. The grey line represents the bridge, the red dots represent GPS points, the yellow dot represents capture & tagging location, the faded white circles represent core 50% home ranges.

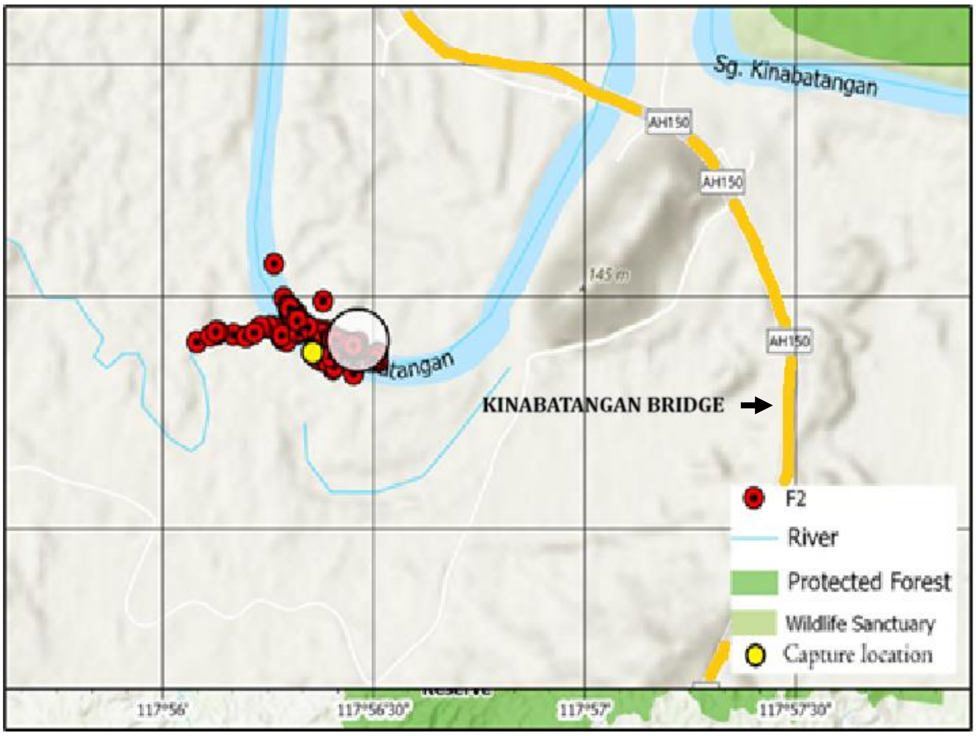


Figure 3.12. Movement of female F2 relative to the man-made bridge over the Kinabatangan River. The grey line represents the bridge, the red dots represent GPS points, the yellow dot represents capture & tagging location, the faded white circles represent core 50% home ranges.

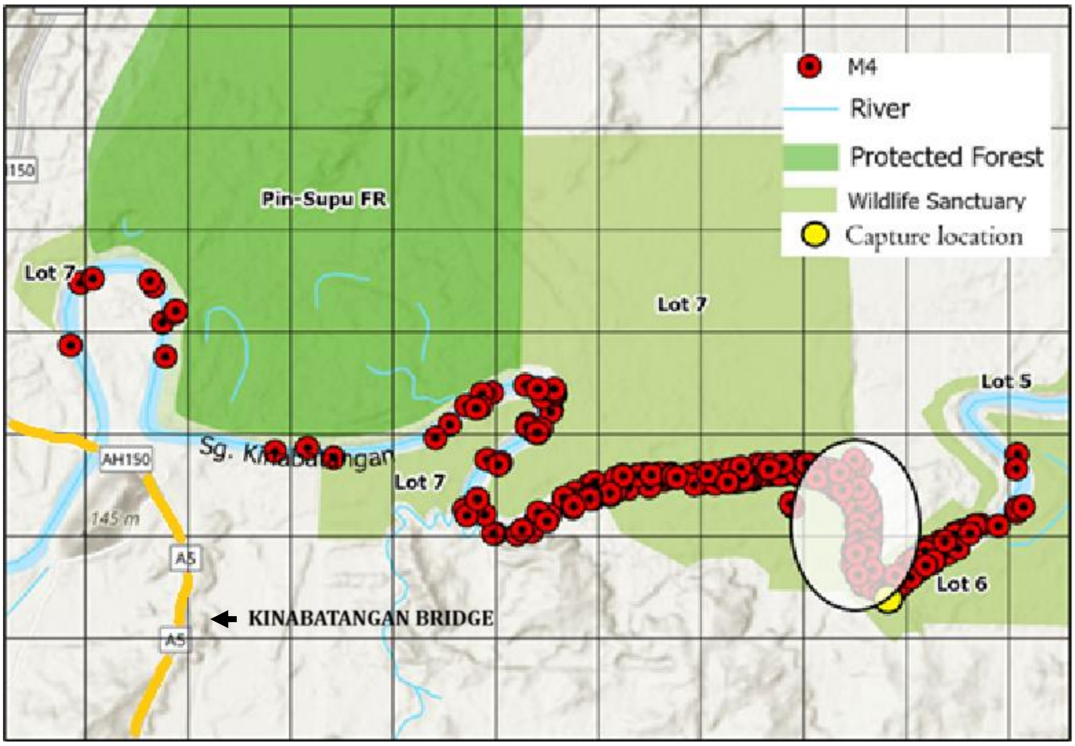


Figure 3.13. Movement of male M4 relative to the man-made bridge over the Kinabatangan River. The grey line represents the bridge, the red dots represent GPS points, the yellow dot represents capture & tagging location, the faded white circles represent core 50% home ranges.

3.4 Discussion

This chapter enhances our understanding of crocodilian movement patterns in the Kinabatangan River, contributing valuable insights into their ecological dynamics in a rapidly changing environment. The presence of breeding-sized adults within the Lower Kinabatangan Wildlife Sanctuary (LKWS) emphasizes the importance of this region as a potential sanctuary for crocodiles amidst increasing anthropogenic pressures. Recent research in similar ecosystems has shown that fragmented habitats can alter movement behaviours and home range sizes in crocodilians (Aiyer *et al.*, 2022). Understanding these responses not only provides a basis for effective management strategies but also highlights the resilience of crocodilian populations in adapting to human-modified landscapes (Sullivan *et al.*, 2020).

No individuals were recaptured throughout the study period. This aligns with findings from previous studies indicating that crocodiles can become trap-shy following initial capture (Burgess *et al.*, 2019). This behaviour may stem from learned aversion to traps, influenced by negative experiences during the capture process. Similar patterns have been observed in other species, where previous capture experiences lead to increased wariness and avoidance behaviours (Parker *et al.*, 2022). The implications of this for population monitoring efforts are important as it suggests that traditional capture-mark-recapture techniques may underestimate population sizes. As such, alternative methods such as remote sensing or camera traps may provide more accurate population estimates.

Recent research indicates that as human populations expand into crocodilian habitats, the likelihood of encounters and subsequent injuries increases, potentially threatening the survival of these reptiles (Charruau *et al.*, 2021). Such conflicts are particularly pertinent in regions like Sabah, where agricultural expansion and habitat destruction are prevalent. Strategies that promote coexistence between humans and crocodiles, such as community education programs and the establishment of buffer zones, are essential for mitigating these conflicts and ensuring the long-term conservation of crocodilian populations in the area.

In Zimbabwe, education campaigns were launched to raise awareness among local communities about *C. niloticus* behaviour and safety precautions when living near water bodies. These campaigns were carried out to reduce negative interactions by promoting safe practices and fostering an understanding of crocodile ecology (Matanzima *et al.*, 2022).

Similarly, in Australia, the creation of buffer zones has proven effective in minimizing encounters by removing "problem crocodiles" from areas commonly used by humans, ensuring both human safety and the preservation of crocodile populations (IUCN Crocodile Specialist Group). These approaches emphasize the importance of proactive management in reducing conflicts and promoting coexistence.

This study also highlights the need for ongoing monitoring and research to inform conservation strategies in light of changing environmental conditions. Studies on crocodilian movement patterns and habitat use in human-impacted landscapes are limited but critical for developing effective management plans (Coleman *et al*., 2024). Further research should aim to explore not only the movement ecology of these animals but also their behavioural adaptations to changing conditions. Understanding the interplay between habitat availability, human interactions, and crocodilian behaviour will be vital for the successful conservation of these apex predators in Borneo and beyond.

Distance Travelled

In this study, the movement and home range metrics of all tagged individuals were assessed, revealing notable differences between male and female crocodiles in terms of distance travelled. Females demonstrated greater total distances travelled on average (~250 km) compared to the males (~220 km), which is 13.64% further in distance than the males. Graham *et al*. (2012) noted that the total distance travelled by males *C. johnstoni* in northern Australia averaged around 350 km. The average Rate of Movement (ROM) for males however was consistently higher (4.36) than that of females (2.31), indicating that males moved about 89% more than females.

A strong positive correlation was observed between ROM and home range size ($r = 0.834$, $p < 0.01$), indicating that individuals with higher rates of movement tend to occupy larger home ranges. However, the correlations between body size and ROM ($r = -0.049$, $p = 0.95$) and body size and home range size ($r = -0.087$, $p = 0.85$) were not statistically significant. In a study of *C. porosus* in Australia, the researchers found that the average ROM for male individuals was approximately 3.2 km/day, while females showed a slightly lower average of 2.5 km/day (Limpus *et al*., 2002). Movement ecology studies of *C. porosus* in Papua New Guinea indicated an average ROM of 3.5 km/day for males and 2.1 km/day for females (Klein *et al*., 2016). The males in this study travelled greater distances compared to females, covering up to 1.2 km over a span of six months. Another study on *C. porosus* movement in human-altered habitats in northern Australia reported an average ROM of 2.3 km/day for females and 3.1 km/day for males (Fukuda *et al*., 2019) with males travelling around 600 km and females around 350 km over a tracking period of 90 days. These studies show that male movement is 28% - 66% higher than females, demonstrating a consistent trend in the distance travelled and ROM that aligns closely with the results observed in the current study. The average ROM recorded for male crocodiles across these studies generally falls within a comparable range to the higher values noted in this research, as compared to female crocodiles.

Male crocodiles often exhibit longer travel distances and higher ROM compared to females due to several ecological and behavioral factors. One primary reason for this difference is the search for mates, particularly during the breeding season. Males tend to cover larger territories in pursuit of females, leading to increased movement as they compete for access to potential mates (Klimley *et al*., 2003). This behavior is commonly observed in various crocodilian species, where males display greater roaming patterns as they establish dominance and seek out breeding opportunities (Mazzotti *et al*., 2009). Moreover, the larger body size of males can contribute to their greater mobility, as larger individuals may have fewer natural predators and can exploit a wider range of habitats in their quest for resources and mates (Fergusson *et al*., 2001).

The differences in reproductive strategies between the sexes may also play a role in different movement patterns. Female crocodiles tend to invest profoundly in reproductive success by focusing on nesting activities and maternal care, which requires them to conserve energy and remain close to nesting sites, resulting in smaller rates of movement. For instance, *C. porosus* females were observed to stay within a specific area during the nesting season to guard their nests and ensure the survival of their offspring (Mason *et al*., 2020). This strategy not only helps protect the eggs from predators but also allows mothers to respond quickly to any threats. Similarly, Klein *et al*. (2019) found that female *C. acutus* exhibited limited movements during nesting, prioritizing energy conservation to optimize reproductive output.

In contrast, males may prioritize foraging and territorial expansion, which could explain the observed trends of greater distances traveled and higher ROM in males compared to females. This behavior aligns with findings by Fujisaki *et al*. (2014), who noted that male crocodiles consistently outpaced their female counterparts in terms of movement, likely reflecting the inherent reproductive strategies that drive such behaviors in crocodilian species.

Generally, the movement patterns of *C. porosus* in this study reinforces the notion that these reptiles possess inherent movement capabilities that facilitate their survival and reproductive success. This consistency across different studies underlines the ecological adaptability of crocodiles, which may be linked to evolutionary traits that enhance their locomotion in various environments. The converging evidence in movement patterns also suggest that crocodilians around the world share comparable behavioral traits, irrespective of their geographical origins and the specific habitat structures they inhabit. Despite variations in environmental conditions, such as the availability of prey and habitat fragmentation, the observed movement strategies, as noted in studies conducted in Australia, America, and Southeast Asia, indicate that *C. porosus* likely maintains similar behavioral adaptations. These adaptations could be vital for their survival, enabling them to navigate and exploit resources efficiently in diverse ecosystems.

Home Range

The Kernel Utilization Distribution (KUD) analysis revealed that male *Crocodylus porosus* exhibited larger average total home range sizes (90% KUD) compared to females (males = 13.46 ± 16.33 km^2, females = 10.08 ± 10.86 km^2). However, this difference was not statistically significant ($t = 0.371$, $p = 0.366$). Similarly, the core home range sizes (50% KUD) showed that males had larger average core ranges compared to females (males = 2.48 ± 3.61 km^2, females = 1.93 ± 1.69 km^2), but again, the difference was not statistically significant ($t = 0.321$, $p = 0.314$). This suggests that, while males may have larger spatial use on average, the observed differences indicate that the variation in home range sizes between sexes could be influenced by other factors beyond sex-specific ecological behaviors.

The association of body size and home range in crocodilians, particularly in *Crocodylus porosus*, presents a complex picture. Generally, one might expect that larger individuals would occupy larger home ranges due to increased energy needs, greater foraging areas, or territorial requirements. In the current study, this pattern appears to hold true for females, where F1, the largest female at 396 cm, has the largest home range of 26 km^2, suggesting that larger females may require more wide territories for nesting and foraging, which aligns with findings from other studies. For instance, Klein *et al*. (2019) found that larger females *C. acutus* had larger home ranges, reflecting their reproductive strategies, as larger females potentially need more space to accommodate nesting activities.

The case for male individuals presents a contrasting scenario. In this study, the smallest male, M5 at 356 cm, has the largest home range of 41 km². This unexpected result indicates that factors other than size such as social dynamics or mating strategies, equally play a role in determining the home ranges of male crocodiles. Research by Read *et al.* (2019) highlighted that male crocodiles often exhibit larger home ranges as they roam extensively in search of mates and resources, regardless of their size.

This difference aligns with the expectation that male crocodiles tend to occupy larger territories to maximize their access to mates and resources (Thorbjarnarson, 1992). For instance, a study by Read *et al*. (2019) on *C. porosus* in Australia found that males had larger home ranges than females, with males averaging around 50 km² while females averaged approximately 20 km². Similarly, two other studies on *C. acutus* in Florida and *C. intermedius* in Venezuela documented KUDs ranging from 25 km² to 45 km² for male individuals and 10 km² to 20 km² for female individuals (Gonzalez *et al.*, 2019; Klein *et al.*, 2019). The movements of male *C. porosus* in Northern Australia reported extensive home ranges that allowed them to engage in territorial behaviours and mate searching.

The observed variability in home range sizes among male crocodiles suggests that factors beyond physical size, such as territorial behaviour, resource distribution, and mating strategies, play important roles in shaping these patterns. Some maintain stable home ranges, while others adopt nomadic strategies. These behaviours are often influenced by social dynamics and environmental conditions rather than size alone (Barham *et al.*, 2023). Additionally, studies on crocodilian social structures highlight that dominance hierarchies are not solely determined by size; factors such as individual behaviour, experience, and environmental context also contribute to dominance and territory establishment (Baker *et al.*, 2021). This complexity of multiple ecological and social factors is important when examining home range variability in crocodilian populations. While size may influence home range to some extent, behavioural strategies, resource availability, and mating dynamics are critical determinants in the spatial ecology of crocodiles.

One possible explanation for the lack of statistical significance in the present study is the high variability in home range sizes within both sexes, particularly among males. For example, in the total home range analysis, M5 exhibited the largest home range at 41.7 km², while M1 had the smallest at 1.4 km², indicating considerable individual variation. Similarly, in the core home range analysis, M5 displayed the largest core range at 9.2 km², while M1 had the smallest at 0.3 km². Conversely, some females, such as F1, exhibited total and core home range sizes that were comparable to or larger than some males, further contributing to the overlap between groups.

The variation in tracking durations among individuals may also play a role. Tracking periods ranged from 15 days (F4) to 224 days (F1), which likely influenced the observed home range sizes. Longer tracking durations, such as those for F1 and M5, are more likely to capture the full extent of spatial use, resulting in larger home ranges. Conversely, shorter tracking periods, such as for F2 (39 days) and M5 (28 days), may underestimate home range sizes, particularly for highly mobile individuals. Studies, such as Kay (2004), have highlighted the importance of longer tracking periods in accurately estimating crocodile home range sizes, as short durations often fail to capture the full extent of movement patterns.

Environmental constraints may also have contributed to the lack of significant differences. Habitat limitations, such as restricted connectivity, resource availability, or anthropogenic barriers (e.g., bridges), could homogenize spatial use across sexes. For instance, Fukuda *et al.* (2013) found that the presence of barriers like dams and urban structures can restrict crocodile movements, thereby reducing observable differences between males and females. The study area in this research may impose similar constraints, particularly in regions where core ranges are located near anthropogenic structures, as observed for F1.

Finally, the relatively small sample size (five males and four females) reduces the statistical power of the analysis, making it harder to detect significant differences even if they exist. Similar limitations were noted by Brien *et al.* (2017), who emphasized the need for larger sample sizes to improve the reliability of spatial ecology studies. Additionally, the observed overlaps in home range sizes between males and females in this study align with findings from Klein *et al.* (2016) in Papua New Guinea, where individual variability often masked sex-specific patterns. While the differences in total and core home ranges between males and females were not statistically significant ($p > 0.05$), males still tend to have larger ranges, which aligns with findings from other studies as mentioned above.

Distance to Centroid

The distance to centroid analysis provides valuable insights into the movement patterns of the tagged crocodiles. The graphs created illustrate the varying distances each individual travelled from their respective centroids over time, with the peaks indicating the maximum distances reached during their excursions, and the red dots representing the specific locations of these individuals, highlighting their positional data. In examining the peaks for females, it was observed that F3 demonstrated the most extensive movement, reaching distances of almost seven kilometers from the centroid, particularly evident in early August. This suggests that while F3 primarily remained close to the centroid, she engaged in occasional longer excursions, as evidenced by the numerous peaks in the graph. These movements might correspond to foraging trips or exploratory behaviour, although the overall pattern indicates a tendency for F3 to prioritize her core habitat.

Individual F1 indicates a highly dynamic movement pattern throughout the study period. The recorded distances highly fluctuated, with notable peaks of four kilometres. F2's movement, although relatively more restrained compared to F1 or F3 with the maximum recorded distance of about 550 meters, showed same patterns of exploratory behaviour. The distance to centroid graph for F4 presents a distinct pattern in her movement behaviour. There is a single peak recorded at over three kilometres, indicating a brief excursion away from her core area. However, following this peak, F4 predominantly remained within a localized range, implying a strong affinity for her core area.

The clustering of the red dots around the centroid area for the female crocodiles shows their primary home range, where they spend most of their time. This concentration suggests a preference for localized habitats that likely offer essential resources such as shelter, food, and suitable conditions for nesting. A study on the spatial ecology of female *C. niloticus* has shown that nesting females maintain smaller home ranges during the nesting season, focusing their activities around nesting sites to ensure proximity to necessary resources and protection for their offspring (Combrink, 2015). Similarly, research on female *C. porosus* has demonstrated that they exhibit high nest fidelity and select nesting sites based on the availability of optimal environmental conditions, further emphasizing the importance of localized habitats that offer critical resources for nesting success (Baker *et al*., 2019).

The proximity to the centroid reflects the females' tendency to remain in familiar environments, or in other words, site fidelity, reducing the risk of predation (Read *et al*., 2019). In essence, this clustering indicates a strategy for energy conservation, as remaining close to the centroid minimizes unnecessary movement while maximizing access to necessary resources.

In contrast, the sparse clustering observed towards the peaks of the graphs indicates periods of extended movement away from the centroid. These peaks represent the furthest distances the crocodiles traveled from their core areas, or temporary excursions that could be motivated by various factors, such as searching for food, avoiding disturbances, or exploring potential nesting sites. The less frequent nature of these excursions, as indicated by the sparse clustering, suggests that such movements are occasional trips that might coincide with specific ecological or environmental pressures. Overall, the combination of dense clustering at the centroid and sparse peaks highlights a dual pattern of behavior: a strong tendency towards core habitats balanced by occasional exploratory movements, reflecting the complex dynamics of crocodilian habitat use and movement strategies. Similar patterns were documented in other studies of *C. porosus*, where females exhibit a strong affinity for core habitats, punctuated by exploratory movements (Cott, 2010; Gonzalez *et al*., 2019).

The distance to centroid analysis also reveals a notable pattern in the exploratory trips of female individuals, particularly during the months of May to August. Evans (2016) indicates that nesting in Kinabatangan River typically occurs during the dry season, which is critical for ensuring the safety and viability of the nests. Specifically, nesting period aligns with the months of May to August, which allows females to select suitable sites. For F1, significant peaks in distance were observed during this nesting season, which is consistent with the dry season in Malaysia when female crocodiles actively seek suitable nesting sites. This period allows for better access to elevated areas along riverbanks, reducing the risk of flooding, which is crucial for the survival of the eggs (Luiselli *et al*., 2006). The peaks in F1's movements during this timeframe underscore the importance of this period for reproductive activities. Similarly, F2 exhibited notable peaks in July and August, aligning with the nesting season as well. For F3, peaks observed in August and September suggest that this female was also engaging in exploratory behavior associated with nesting activities, potentially moving to find optimal locations for laying her eggs. In contrast, F4's single peak in November suggests a different behavioral response, as she remained close to her centroid from September onwards. This behavior corresponds to the onset of the rainy season, during which conditions become less favorable for nesting, prompting her to minimize movement and prioritize core habitat utilization.

All male crocodiles (M1-M5) displayed larger distances to the centroid compared to their female counterparts. M1 demonstrated notable peaks primarily from July to August, indicating a period of heightened activity and exploration. This aligns with the nesting season, suggesting that M1 may be actively seeking mates or territories during this time. In contrast, M2 presents a different pattern, with a significant peak in March and closer proximity to the centroid during February, indicating that it may have been utilizing its core area more intensively before an exploratory trip. Individuals M3 and M4 exhibit the same patterns, with multiple peaks occurring from October to December. Individual M5 presented a mixed pattern with few peaks in March and some points closer to the centroid, suggesting that while it engaged in exploratory excursions, it also maintains a degree of habitat fidelity. The absence of clustering near the centroid for these males suggests a consistent exploratory behaviour, potentially in search of resources or mates, indicating a more extensive range of movement compared to females.

A comparison of the average distance to the centroid between male and female *C. porosus* revealed that females had a slightly higher mean distance (3.65 km ± 2.59) compared to males (3.2 km ± 1.72). However, t-test showed that the difference was not statistically significant (t = 0.381, p=0.381), suggesting that on average, males and females in this study exhibited no significant sex-based differences in their spatial distribution around core areas. The higher standard deviation for females reflects greater variability in their distances to the centroid, which may be influenced by individual differences or environmental factors.

The mapping of home ranges for individual crocodiles revealed some differences in habitat use, particularly between those that ventured off the main river body and those that remained within forested sections. Individuals F1, M3, and M5 were the only individuals that exhibited movements that extended beyond the primary river channel, utilizing nearby habitats that include unprotected forest, oxbow lakes and areas adjacent to oil palm plantation, respectively, suggesting a degree of adaptability and resourcefulness in these individuals, potentially driven by factors such as prey availability or competition within their core habitats. The preference for a diverse habitat can enhance their chances of survival by allowing access to a variety of resources, including nesting sites and feeding opportunities.

Individual F1, the largest female among the tagged crocodiles, exhibited a unique movement pattern that took her deep into the forested areas of her habitat. This behaviour may be attributed to her size, which potentially provided her with greater physical capabilities to navigate through more challenging environments compared to smaller individuals. Larger female crocodiles often require more extensive ranges for foraging, nesting, and avoiding potential predators or competitors. Cott (2010) found that larger females *C. niloticus* utilized more diverse habitats, venturing into terrestrial environments for nesting purposes. Females that do not venture as far into the forest may do so due to a variety of factors, including habitat preference, reproductive strategies, or physical limitations. Smaller individuals may prioritize remaining closer to water bodies, where food is more readily available, thus reducing their risk of predation (Read *et al.,* 2019). F1's extensive movements not only highlighted her unique capabilities but also stress on the complex interplay between size, habitat utilization, and ecological dynamics in female crocodilian behaviour.

Individual M3, the largest male crocodile in the study, exhibits a broad habitat use by exploring into oxbow lakes. This could be motivated by the search for prey and suitable basking sites, as larger males require greater foraging areas to sustain their energy needs (Campbell *et al.*, 2013). Oxbow lakes, with their rich biodiversity, provide ideal feeding grounds, supporting a variety of aquatic species (Ortmann-Ajkai, 2019). Additionally, these areas offer optimal basking conditions, which is important for thermoregulation in ectothermic reptiles like crocodiles (Webb *et al.,* 1983; Grigg & Kirshner, 2007). Furthermore, the tendency of larger male crocodiles to venture into diverse habitats, can be attributed to their territorial nature. M3’s movements possibly reflect the need to establish and defend a territory. This aligns with previous studies indicating that male crocodiles exploit various habitats during their movements to maximize their chances of reproductive success and resource acquisition (Cott, 2010; Klein *et al*., 2019). M5, the smallest male in the study, exhibited a distinctive movement pattern characterized by a core home range situated predominantly in forested areas, yet his travel routes ventured close to oil palm plantations, indicating a reliance on both habitat types to meet his ecological needs.

Previous studies show that crocodiles often adjust their habitat use in response to environmental changes and resource availability. For instance, Smith *et al.* (2016) showed that smaller *A. mississippiensis* exhibited greater flexibility in habitat use, which allowed individuals to adapt to surrounding land-use changes, such as the presence of agricultural areas. This adaptability is crucial for survival in fragmented habitats, as it can increase access to diverse food sources and shelter options. The remaining tagged individuals reflects this pattern, where their core home ranges predominantly reside in forested areas, but were also observed utilizing river sections adjacent to oil palm plantations, indicating an adaptability to varied habitats. Individual F4, in particular made the decision to venture into a tributary and established a core home range in an unprotected forest area adjacent to oil palm plantations. This is a rather striking observation, although this could have potentially been a strategy for finding refuge or a temporary escape route, especially since F4 was monitored for only 15 days. As highlighted by Panda *et al*. (2023), crocodiles may exhibit altered movement behaviours immediately following capture, as they seek refuge to minimize perceived threat. Hence, limited monitoring periods may not fully capture the crocodile's natural movement patterns, which could evolve over time as it acclimatizes to its surroundings.

Crocodilians, including *C. porosus,* typically exhibit a strong preference for forested habitats such as mangroves, wetlands, and riverine environments. These natural habitats provide essential resources such as shelter, food, and suitable conditions for nesting (Evans *et al.*, 2016). Studies have shown that these reptiles are commonly found in areas of low human disturbance, allowing them to thrive in their preferred ecological niches. However, their adaptability to changing environments make them occasionally venture into agricultural areas, including rice paddies and plantations, particularly during high water levels or seasonal migrations. For example, *C. niloticus* in the Okavango Delta and *C. mindorensis* in the Philippines have been observed utilizing adjacent agricultural fields, especially when their primary habitats are less accessible due to flooding (Thorbjarnarson, 1992; Manola & Alcala, 2015).

This tendency to explore agricultural landscapes can be attributed to various ecological pressures, including the search for prey and optimal basking sites during wet or dry seasons in these modified environments, they often find abundant food sources, including small mammals and fish that thrive in such areas. For instance, studies have observed crocodiles frequenting plantation areas, indicating that these habitats can provide essential resources (Evans *et a*l., 2016). Additionally, female crocodiles have been observed nesting in agricultural lands, such as oil palm estate ponds. Research utilizing drone technology has identified crocodile nests in close proximity to oil palm plantations, suggesting that low to medium levels of human disturbance do not deter successful nesting (Evans *et al*., 2015). This flexibility demonstrates their resilience and adaptability to changing ecological conditions. This adaptability also raises important questions about the influence of anthropogenic changes on crocodile behaviour, particularly in relation to infrastructure development. The construction of man-made structures, such as bridges, can significantly alter crocodilian movement patterns and habitat use, potentially disrupting established migration routes and access to critical resources.

Bridges as an anthropogenic barrier

None of the crocodiles tagged in this study showed signs of passing under the 350-metre-long man-made bridge built over the Kinabatangan River. More obviously, the movement patterns of individuals F1, F4, and M2 reveal a very important behavioural response to the presence of this structure. All three crocodiles exhibit consistent usage of their habitats, traversing along the river and utilizing areas up to the bridge's location. However, their movements are noticeably interrupted right at the bridge, as none of them cross under it to access the other side of the river. It almost seemed as though the bridge served as a barrier that restricts movement (Figure 4.9). The movement of individuals F2 and M3 reveal similar avoidance towards the bridge. While these individuals do not approach the bridge as closely as F1, F4, and M2, they still demonstrate a tendency to stay away from it.

Fukuda *et al.* (2019) investigated the movement patterns of *C. porosus* in northern Australia and found that none of the eight tracked crocodiles exhibited overland movement between water bodies. Additionally, none of them crossed the Cobourg Peninsula, despite a strong inclination in some individuals to return to their original capture sites. This observation supports the notion that the peninsula acts as a barrier to the dispersal of these individuals, although the specific reasons for this behaviour remain unclear. Another study investigating the population dynamics of *C. niloticus* in Loskop Dam, South Africa found that dam construction led to habitat alteration, including flooding of basking and nesting areas (Sukumar & Sinha, 2018). This resulted in a significant decline in crocodile numbers due to reduced recruitment and increased pollution levels in remaining suitable habitats. The altered spatial distribution forced crocodiles into areas with higher pollution exposure, which contributed to health issues and periodic die-offs within the population. While these studies are focused on the direct negative impacts of certain structures on the movement of crocodiles and habitat use, the impact of overhead structures, such as bridges, may similarly affect crocodile behavior.

Even though the Kinabatangan bridge crosses the river from one side to the other, its presence still disrupts the surrounding environment. The potential influence of noise and vibrations from heavy traffic on crocodile movement patterns is not fully understood. While some studies suggest that crocodiles can detect and be affected by low-frequency vibrations, leading to stress or altered behaviours (Ghai, 2019), direct evidence linking these disturbances to specific avoidance behaviours near infrastructure like bridges is limited. In this study, five individuals exhibited avoidance behaviours toward the bridge; however, this observation is correlational, and causation cannot be conclusively established. These findings highlight the importance of considering how infrastructure may impact wildlife connectivity and conservation efforts. Implementing mitigation strategies, such as wildlife passages, can facilitate safe movement across man-made barriers, promoting ecological connectivity.

This also has implications on population dynamics, ultimately resulting in the fragmentation and isolation of individuals. This scenario would disrupt the natural movement patterns of crocodiles, hindering their ability to disperse, locate mates, and access critical habitats. Fragmentation is particularly concerning as it can create subpopulations that are less genetically diverse, increasing the risk of inbreeding and reducing the overall genetic health of the population (Frankham *et al.*, 2010). The reduction in genetic variability eventually diminishes the resilience of the population to environmental changes, diseases, and other stressors (Hansen *et al.*, 2011). In essence, barriers such as bridges can impede the movement of crocodilians, potentially leading to long-term repercussions for their genetic diversity and overall survival. Disruptions in movement can hinder gene flow, resulting in genetic isolation and reduced genetic diversity, which may compromise population resilience. For instance, a study on *C. porosus* in Australia found that geographic barriers (Cobourg Peninsula) disrupted movement and dispersal, leading to distinct genetic structuring among populations (Fukuda *et al.*, 2019).

Although limited research has been conducted on the effects of human-induced changes on crocodilians, these few existing studies suggest that these reptiles are highly sensitive to environmental disturbances, which can significantly alter their movement and habitat use patterns (Frankham *et al.*, 2010; Hansen *et al.*, 2011; Fukuda *et al.*, 2019; Ghai, 2019). This emphasizes the necessity of understanding how human activities impact crocodilian behavior and habitat use, as such changes can have profound implications for their conservation and management. As urbanization and infrastructure development continue to expand, it becomes increasingly important to develop strategies that mitigate these impacts, ensuring the survival of these species and maintaining the ecological integrity of their habitats. Ultimately, fostering a deeper awareness of the interactions between crocodilians and human-altered landscapes is crucial for implementing effective conservation measures that balance ecological health with human needs.

The Kinabatangan River, with its unique and diverse ecosystem, plays a crucial role in shaping the movement patterns and home ranges of the crocodiles. Its intricate network of waterways, floodplains, and forested areas supports a rich array of wildlife and is vital for the ecological health of the region. Despite the presence of a substantial *C. porosus* population, the future of this ecosystem hangs in the balance as human disturbances and human activities, such as the construction of man-made structures, threaten to disrupt the delicate balance of these habitats. Preserving key hotspots along the river is essential to ensure the continued survival of crocodiles and other apex predators, which play a critical role in maintaining the structure and function of their ecosystems (BiologyInsights Team, 2024).

Crocodiles, as apex predators, are integral to the health of the Kinabatangan River ecosystem, controlling prey populations and thus contributing to biodiversity (Thorbjarnarson, 1992). The same considerations apply to other rivers in Sabah, where habitat preservation is essential to sustaining the ecological integrity of these areas. Without careful management and protective measures, the unique wildlife and diverse habitats that characterize the Kinabatangan River may decline, jeopardizing not only the crocodile population but also the myriads of species that rely on this rich environment for survival. Conservation efforts must prioritize maintaining connectivity and protecting natural habitats to ensure the resilience of crocodilian populations and the ecosystems they inhabit (Fukuda *et al.*, 2019).

CHAPTER 4

Genetic Diversity of the Estuarine Crocodile in Sabah

4.1 Introduction

Genetic diversity is the foundation for species and ecosystem diversities. The ultimate objective of conservation genetics is to apply the knowledge of genetics in reducing the risk of extinction. Conservation genetics involves genetic factors that cause scarcity, endangerment and extinction, and genetic management to aid in reducing the effects of these factors. It also encompasses the use of genetic variation to understand the history of threatened species and their taxonomic uncertainties (Frankham *et al*., 2019).

For many species, genetic diversity occurs in three hierarchies, which are, genetic variation within an individual, genetic variation among individuals in the same population, and the genetic variation among populations of the same species that are either geographically connected or disconnected from each other (Wright, 1931). These variations are products of evolutionary occurrences such as genetic drift, gene flow, natural and sexual selection, interbreeding etc. (Avise, 2004). The amount of genetic diversity available in a population is the raw material for evolutionary changes to shape that population. Thus, it is critical that the genetic diversity of populations is conserved to ensure short-term and long-term survival of the populations and species as a whole (Allendorf & Leary, 1988).

Small and isolated populations, whether in the wild or in captivity, are prone to a gradual loss of genetic diversity due to the combined effects of inbreeding and genetic drift (Amos & Balmford, 2001). The recovery of genetic diversity in these populations is typically a slow process, as it relies on mutation to generate new variation or requires genetic input through mechanisms such as gene flow or translocations. Therefore, the optimal strategy is to preserve genetic diversity by maintaining populations that are large and well-connected to other populations, which helps to mitigate the effects of genetic drift and inbreeding (Scribner *et al*., 2016). Moreover, genetic data play a crucial role in conservation efforts by providing essential insights into population structure, connectivity, adaptive capacity to environmental changes, and hybridization events (Hohenlohe *et al*., 2020).

The IUCN SSC Crocodile Specialist Group (CSG) emphasizes the need for research on population genetics of crocodilians to evaluate their genetic diversity and consequently develop management programs for them (Ross, 1998). The inferences derived from that type of genetic data provide information about population structure, gene flow, migration patterns etc., all vital aspects for the development and implementation of conservation programs for crocodilians in their resident habitats as well as across their distribution range.

Several studies examining the population genetics of crocodilian species have been undertaken, such as Morelet's crocodile (*C. moreletii*) (Dever *et al*., 2002; González-Trujillo *et al.*, 2012), American alligator (*A. mississippiensis*) (Glenn et al., 2002) and American crocodile (*C. acutus*) (Cotroneo, 2010), broad-snouted caiman (*Caiman latirostris*) (Saidman *et al.*, 2012) and the Nile crocodile (*C. niloticus*) (Hekkala *et al*., 2009; Schmitz *et al*., 2003). These studies have provided valuable understandings of gene flow, population structure and genetic diversity of crocodile species (Versfeld, 2016; Muniz *et al.*, 2018). However, the majority of genetic studies carried out on *C. porosus* have been focused predominantly on farmed and captive-bred populations (Luck *et al*., 2012). A large amount of these studies uses microsatellite markers to understand population diversity in *C. porosus*, with many such studies detecting genetic differences in wild *C. porosus* populations in various countries (Miles *et al*., 2009). These studies have provided valuable insights into the evolutionary history and dynamics of *C. porosus* populations in South East Asia and Oceania including countries such as Australia, Philippines, Thailand and Indonesia which include wild *C. porosus* populations (Luck *et al*., 2012; Lapbenjakul *et al*., 2017). Several molecular genetic studies on *C. porosus* have also been carried out in Sabah's neighbouring state Sarawak using microsatellite and mitochondrial DNA markers (Kasim, 2011; Nadarajan *et al*., 2023). However, in Sabah, these insights remain uncertain due to limited genetic studies carried out on the wild populations of *C. porosus*.

Wild populations are a major challenge to population genetic analysis, as development of genetic markers is a problem that has effectually excluded many species from consideration for research (Davey & Blaxter, 2010). The development process of these markers typically includes marker discovery, the identification of polymorphic (variable) markers using a discovery panel, and their application across populations. Due to the issue of identifying polymorphic markers using a relatively small set of samples, unless these are quite diverse (a not know fact when staring the marker development process) and they represent a wide range of the species distribution (i.e. to maximise capturing genetic variation), it is likely that the markers developed may not represent the genetic variation of other populations not included in the marker discovery panel. In such instances studies of populations different from those used in the marker discovery panel can be limited due to issues derived from ascertainment bias such as the inference of apparent reduced genetic diversity and higher inbreeding (Davey & Blaxter, 2010).

Common markers used in genetic studies include microsatellites and mitochondrial DNA (mtDNA), single nucleotide polymorphisms (SNPs) and insertion-deletion polymorphisms (indels). Despite being widely used, the process of developing these markers can be costly in terms of funding and it usually takes time (Davey & Blaxter, 2010). While a plethora of markers have been further developed through the genomics revolution, the use of mitochondrial DNA sequencing remains an important way to rapidly and cheaply collect data for lots of individuals. Mitochondrial DNA is highly abundant in almost all tissues as mitochondria occur in high copy numbers within each eukaryotic cell, and because each mitochondria has a copy of its circular DNA, for each single cell eukaryotic DNA copy there can be thousands of mitochondrial DNA copies. Furthermore, after eukaryotic cells breakdown and disappear when they die, mitochondrial DNA may remain in the tissue long after the nuclear DNA is lost (Panko, 2017). Additionally, mitochondrial DNA presents a higher substitution rate than nuclear DNA enabling a faster accumulation of polymorphisms that can be used to study a species genetic variation across space and time (Orozco-terWengel *et al*., 2008).

The development of high throughput sequencing (previously known as Next Generation Sequencing) opened the doors to the possibility of rapidly collecting large amounts of genome-wide data for multiple samples, alas, despite of the per sequenced base price fall during the last decade, doing whole genome sequencing for large quantities of individuals (e.g. 100 or more) remain prohibitive (Biscarini *et al*., 2018). A more recently described method called restriction site-associated DNA sequencing (RADseq), detects and scores thousands of genetic markers randomly dispersed across the target region from a group of individuals (Baird *et al*., 2008). It can be used to undertake population genetic studies that have limited, or no sequence information of a species. This by itself is a huge advantage over other markers.

The importance of genetic research on *C. porosus* in Sabah cannot be overstated. For a species like *C. porosus*, which faces threats from habitat loss, human-wildlife conflict, and illegal hunting, characterising their genetic diversity is crucial to support the species survival. The current study on the genetic diversity and population structure of *C. porosus* in Sabah represents one of the first comprehensive genetic investigations of this apex predator in the region. While crocodiles have been studied globally for their ecology, demography, and conservation status (Crocodile Specialist Group, 1989), the genetic landscape of the Sabah population has largely remained unexplored. By using mitochondrial DNA markers such as ND2, D-loop, 16S, and Cytb, this study provides a foundational understanding of the genetic diversity and structure within and between crocodile populations in the main rivers of Sabah.

Primary objective

To understand the overall genetic diversity of the *C. porosus* population in Sabah.

Secondary objectives

1. To characterize the genetic diversity in populations of *C. porosus* in Sabah.
2. To explore the genetic structure within and among populations of *C. porosus* in Sabah.
3. To determine the evolutionary relationships and demographic history of the *C. porosus* populations in Sabah.

Hypotheses

1. The *C. porosus* population in Sabah is genetically diverse.
2. There are significant population differences among the sampled populations of *C. porosus* in Sabah.

4.2 Methodology

4.2.1 Sample Collection

Tissue samples were collected from 200 unique crocodile individuals between April 2017 and November 2019 across nine rivers in Sabah, as well as from four problematic individuals that were removed from recreational areas (referred to as relocated individuals) in 2020 and 2021 by rangers from the Sabah Wildlife Department. Besides the problematic individuals, eight other adult crocodiles (from the Kinabatangan River) were among the 200 individuals sampled. The remaining individuals consisted of hatchlings and juveniles. Sampling was conducted under ethical guidelines, with access and export licenses obtained from the Sabah Biodiversity Centre (SABC) to collect samples from the wild and to export DNA for laboratory analyses at Cardiff University.

Adult individuals were captured using steel mesh traps (refer to Chapter 3), whereas hatchlings and juveniles (shorter than 1.5 m in length) were hand-captured from a boat. Upon capture, a tissue sample (scute) was taken from the tail of the crocodile and kept in a 50 ml centrifuge tube of 90% ethanol for storage. The GPS location was recorded at capture site before the animal was released back into the water. Figure 4.1 shows the locations from which *C. porosus* samples were obtained from in Sabah.

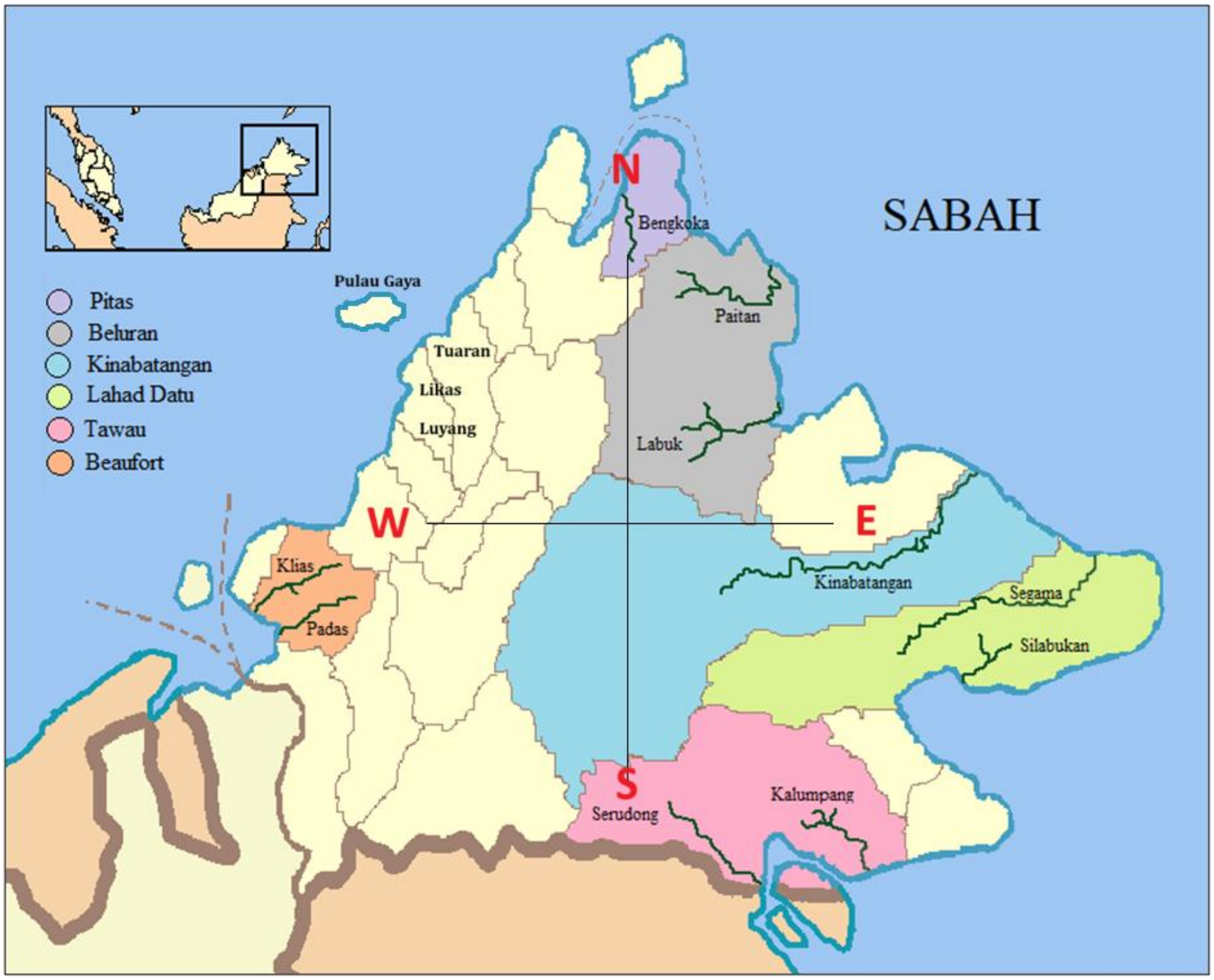


Figure 4.1 Map of Sabah indicating sampling sites. Sampling sites are indicated in green, while the districts are colour-coded. Luyang, Likas, Tuaran and Pulau Gaya represent capture sites of problematic crocodiles.

4.2.2 Mitochondrial DNA

DNA extraction was carried out using a Qiagen DNeasy blood and tissue kit (Qiagen, Venlo, Netherlands). DNA quality and quantity were determined by electrophoresis on 1% agarose gels and also by spectrophotometric analysis using Qubit. For the phylogeographic analysis, four sections of the mitochondrial genome's (mtDNA) were amplified through polymerase chain reaction (PCR) using respective primers: D-loop, Cytochrome oxidase B (CytB), NADH dehydrogenase subunit 2 (ND2), and 16S ribosomal RNA (16S rRNA). These regions were chosen due to their varying rates of mutation, providing a comprehensive understanding of both recent and ancient genetic divergences.

The protocol for PCR reactions consisted of reactions of 15 µl using 2 ng of DNA, 1.5 mM MgCl2, 0.2 mM dNTPs, 0.2 mM of each primer, 1X GoTaq® buffer and 0.02 U/µl GoTaq® DNA polymerase (Promega). The PCR thermal cycle conditions were an initial denaturation at 95°C for 2 minutes, followed by 32 cycles of 94°C for 25 seconds, 48°C for 45 seconds for primer annealing and a PCR product extension at 72°C for 45 seconds. A final PCR product extension was carried out at 72°C for 5 minutes.

Sequencing for the D-loop region was performed by Apical Scientific Sdn. Bhd. (Malaysia) whereas, the sequencing of CytB region, 16S region and ND2 region were performed at the Molecular Ecology and Evolution Laboratory at Cardiff University, UK (Table 4.1). The BLASTn and BLASTx programs (http://blast.ncbi.nlm.nih.gov/Blast.cgi) were used to search nucleotide sequences in the National Center for Biotechnology Information (NCBI) database to confirm the identity of the DNA fragments amplified in the present study. Four additional CytB samples of Sabahan *C. porosus* deposited in Genbank were included in the analyses (accession code 1, 2, 3, 4).

Table 4.1 Locality data for the 32 saltwater crocodile samples used in mtDNA analysis.

Region	**Primer names**	**Primer sequences**	**No. of samples sequenced**
Dloop	L15463 H16260	CGCTGGCCTGTAAGACAGA ACTAAAATTACAGAAAAGCCGAC	100
CytB	cytb_Croc_POTW_F cytb_Croc_POTW_R	ACGAAAATCCCACCCACTCT GGGGACGTAGGCTTATCGAT	96
ND2	ND2_Croc_POTW_F ND2_Croc_POTW_R	ATCCATCGAAGCCTCCACAA CTAGGATTAGGGTGAGGGCG	96
16S	16S_Croc_POTW_F 16S_Croc_POTW_R	CGAATCTGGGCGAGCTACTA CTTTGTGGTGTGGGTCTTGG	96

4.2.3 Genetic Diversity and Haplotype Network

The sequence data were edited using the software GENEIOUS and aligned with the CLUSTAL-W algorithm implemented in MEGA v11 (Tamura *et al*., 2021). The Clustal alignment of each mitochondrial fragment was confirmed by eye and corrected where necessary. Summary statistics of genetic diversity, including haplotype diversity (H), nucleotide diversity (π), and Watterson's estimator theta (θ_W), as well as neutrality tests like Tajima's D, and Fu's F (FS), were calculated using DnaSP v6.12.03 (Rozas *et al*., 2017). These metrics, which are sensitive to demographic changes in populations, were analysed for the entire dataset, individually for each river, and by region (east and west coasts) enabling a detailed assessment of genetic diversity and evolutionary dynamics within and between populations of the study area. Additionally, a visual representation of haplotype relationships was created using an unrooted median joining haplotype network in PopART (Leigh & Bryant, 2015) which illustrates the frequency and relatedness of each haplotype.

4.2.4 Population Structure

The software Arlequin v3.5.2.2 (Excoffier & Lischer, 2010) was used to perform an analysis of molecular variance (AMOVA), in order to obtain a breakdown of the genetic variation between the within population component and the between population component (Excoffier *et al.,* 1992). Arlequin was also employed to compute the fixation index (FST), which Holsinger & Weir (2009) define as the correlation of randomly chosen alleles within the same subpopulation relative to the whole population. This measure reflects genetic variance and is based on Wright's F-statistics (Wright, 1965), quantifying the correlation between random gametes within subdivisions (S) compared to the total population (T). F_{ST} values, which range from zero to one, indicate genetic similarity within populations when values are low and genetic divergence when values are high (Holsinger & Weir, 2009).

4.2.5 Demographic History

Additionally, a mismatch distribution, represented by the distribution frequency of nucleotide pairwise differences between pairs of sequences from a population, was calculated using DnaSP v6.12.03 (Rozas *et al.*, 2017), providing insights into the population's demographic history (Rogers & Harpending, 1996). Ultimately, the mismatch distribution serves as an indicator of population dynamics; a ragged distribution suggests long-term stability, whereas a unimodal distribution typically indicates population expansion (Harpending, 1994). The demographic analysis was complemented with a Bayesian Skyline Plot (BSP) generated with the software Beast v. 2.7.7 (Bouckaert *et al.*, 2019). BSP plots were generated for each mitochondrial DNA fragment and for the concatenated data of the four fragments. The analysis was also repeated by analysing all samples together and separately for those on the Eastern coast of Sabah and separately for those from the Western coast of Sabah. Beast was run for one million steps of the Markov Chain Monte Carlo (MCMC) algorithm as burn-in and nine million additional steps as data collection steps. Convergence of the MCMC algorithm was determined by obtaining Effective Sampling Size that were 200 or higher, by visually inspecting the results of running each analysis five times. The Hasegawa-Kishino-Yano (HKY) model of evolution was applied and a substitution rate of 1.039 $* 10^{-8}$ (Ho & DeWoody, 2008).

4.2.6 Phylogeny

A phylogenetic analysis was carried out with iQTree v2.3.6 (Minh *et al.*, 2020). For this analysis haplotypes of concatenated markers were used defining four partitions (one per marker). The use of multiple mtDNA markers provided additional statistical support than the one that could be obtained with single gene fragment analyses and the reduced patterns of polymorphisms observed in Sabah's crocodiles. iQTree was used to estimate the most suitable substitution rate for each mitochondrial fragment using the Bayesian Information Criterion (BIC). A sequence of Australian *C. porosus* from Australia's Northern Territory (NC008143) was used to identify the placement of the Australian sample relative to the *C. porosus* form Sabah, and a sequence of *C. siamensis* (DQ353946) was used as outgroup.

4.3 Results

Genetic Variation

Mitochondrial DNA sequence was obtained for a total of 100 *C. porosus* samples for four fragments (ND2, 16S, CytB and D-loop). Sequences were carefully trimmed to ensure data quality and consistency, and sequences of low sequence quality were removed from the dataset. The dataset used for the phylogenetic analysis of the entire *C. porosus* population in Sabah was based on concatenated data, comprising 76 samples of 'complete data', which excludes samples with any missing data as indicated in Table 4.2.

Table 4.2 Summary of samples used in phylogenetic analysis after editing.

Region	No. of samples analysed											Sequence length
	KTS	BGS	KGS	KLS	PDS	PTS	SBS	SDS	SGS	Others	Total	
ND2	15	6	9	7	3	7	15	13	9	-	84	780
16S	14	8	15	7	3	10	14	13	10	-	94	906
CytB	14	8	11	7	3	10	15	12	9	-	89	828
D-loop	15	8	15	7	3	10	15	13	10	4	100	661
Concatenated data	14	8	5	7	3	7	12	12	8	-	76	3157

KTS = Kinabatangan, BGS = Bengkoka, KGS = Kalumpang, PDS = Padas, PTS = Paitan, SBS = Silabukan, SDS = Serudong, SGS = Segama, Others = adult individuals captured in the city area.

To provide a detailed insight into the genetic variation observed across the sampled rivers, the results are first presented individually for each of the four mitochondrial markers analysed. For each marker, tables summarizing the genetic diversity metrics, including the number of haplotypes, haplotype diversity (Hd), nucleotide diversity (π), and Theta Watterson (θW), are provided for all rivers (Tables 4.3 – 4.6). These tables highlight the marker-specific patterns of variation across the studied populations, laying the groundwork for the subsequent analysis of the concatenated dataset.

Table 4.3. Summary Statistics of Genetic Variation for Marker 16S. Number of individuals (n), no. of haplotypes (nH), segregating sites (S), haplotype diversity (H), nucleotide diversity (π), Watterson's theta (θ_W), Tajima's D, Fu's F.

River	n	nH	S	H (±SD)	π (±SD)	Θw (±SD)	Taj D	Fu's F	Segregating Site
Kinabatangan (KTS)	14	1	0	0.000	0.000	0.000	0.000	0.000	-
Bengkoka (BGS)	8	1	0	0.000	0.000	0.000	0.000	0.000	-
Kalumpang (KGS)	15	1	0	0.000	0.000	0.000	0.000	0.000	-
Klias (KLS)	7	1	0	0.000	0.000	0.000	0.000	0.000	-
Padas (PDS)	3	1	0	0.000	0.000	0.000	0.000	0.000	-
Paitan (PTS)	10	2	4	0.5556	0.00184	1.06046	2.05672	3.451	187, 274, 556, 780
Silabukan (SBS)	14	1	0	0.000	0.000	0.000	0.000	0.000	-
Serudong (SDS)	13	1	0	0.000	0.000	0.000	0.000	0.000	-
Segama (SGS)	10	1	0	0.000	0.000	0.000	0.000	0.000	-
TOTAL	**94**	**2**	**4**	**0.2711**	**0.00090**	**0.58649**	**0.70186**	**3.738**	**-**

Table 4.4. Summary Statistics of Genetic Variation for Marker CytB. Number of individuals (n), no. of haplotypes (nH), segregating sites (S), haplotype diversity (H), nucleotide diversity (π), Watterson's theta (θ_W), Tajima's D, Fu's F.

River	n	nH	S	H (±SD)	π (±SD)	Θw (±SD)	Taj D	Fu's F	Segregating Site
Kinabatangan (KTS)	15	1	0	0.000	0.000	0.000	0.000	0.000	-
Bengkoka (BGS)	8	1	0	0.000	0.000	0.000	0.000	0.000	-
Kalumpang (KGS)	10	1	0	0.000	0.000	0.000	0.000	0.000	-
Klias (KLS)	7	2	1	0.2857	0.00035	0.40816	-1.00623	-0.095	403
Padas (PDS)	3	1	0	0.000	0.000	0.000	0.000	0.000	-
Paitan (PTS)	10	2	2	0.5556	0.00134	0.70697	1.84427	2.429	40, 718
Silabukan (SBS)	15	2	1	0.4762	0.00058	0.30754	1.12241	1.120	388
Serudong (SDS)	12	1	0	0.000	0.000	0.000	0.000	0.000	-
Segama (SGS)	9	1	0	0.000	0.000	0.000	0.000	0.000	-
TOTAL	**89**	**5**	**4**	**0.3866**	**0.00155**	**1.38334**	**-0.16625**	**1.184**	**-**

Table 4.5. Summary Statistics of Genetic Variation for Marker ND2. Number of individuals (n), no. of haplotypes (nH), segregating sites (S), haplotype diversity (H), nucleotide diversity (π), Watterson's theta (θ_W), Tajima's D, Fu's F.

River	n	nH	S	H (±SD)	π (±SD)	Θw (±SD)	Taj D	Fu's F	Segregating Site
Kinabatangan (KTS)	15	2	1	0.4190	0.00054	0.30754	0.74210	0.909	780
Bengkoka (BGS)	7	2	1	0.2857	0.00037	0.40816	-1.00623	-0.095	730
Kalumpang (KGS)	9	1	0	0.000	0.000	0.000	0.000	0.000	-
Klias (KLS)	7	2	1	0.4762	0.00061	0.40816	0.55902	0.589	780
Padas (PDS)	3	1	0	0.000	0.000	0.000	0.000	0.000	-
Paitan (PTS)	7	5	4	0.9048	0.00305	2.04082	0.82563	-1.177	58, 113, 257, 551
Silabukan (SBS)	14	1	0	0.000	0.000	0.000	0.000	0.000	-
Serudong (SDS)	13	2	1	0.2821	0.00036	0.32225	-0.27429	0.240	780
Segama (SGS)	9	2	1	0.5000	0.00064	0.36794	0.98627	0.849	780
TOTAL	**84**	**13**	**6**	**0.7287**	**0.00232**	**1.79926**	**0.00931**	**-3.911**	**-**

Table 4.6. Summary Statistics of Genetic Variation for Marker D-loop. Number of individuals (n), no. of haplotypes (nH), segregating sites (S), haplotype diversity (H), nucleotide diversity (π), Watterson's theta (θ_W), Tajima's D, Fu's F.

River	n	nH	S	H (±SD)	π (±SD)	Θw (±SD)	Taj D	Fu's F	Segregating Site
Kinabatangan (KTS)	15	1	0	0.000	0.000	0.000	0.000	0.000	-
Bengkoka (BGS)	8	1	0	0.000	0.000	0.000	0.000	0.000	-
Kalumpang (KGS)	15	1	0	0.000	0.000	0.000	0.000	0.000	-
Klias (KLS)	7	1	0	0.000	0.000	0.000	0.000	0.000	-
Padas (PDS)	3	1	0	0.000	0.000	0.000	0.000	0.000	-
Paitan (PTS)	10	2	4	0.5556	0.00253	1.06046	2.05672	3.451	145, 165, 355, 516
Silabukan (SBS)	15	2	1	0.5143	0.00078	0.30754	1.37595	1.253	470
Serudong (SDS)	13	1	0	0.000	0.000	0.000	0.000	0.000	-
Segama (SGS)	10	2	1	0.2000	0.00030	0.35349	-1.11173	-0.339	164
Kota Kinabalu *-Luyang (LGS)* *-Likas (LKS)* *-Pulau Gaya (PGS)* *-Tuaran (TRS)*	4	3	3	0.8333	0.00278	1.63636	1.08976	0.006	145, 165 145, 165, 355
TOTAL	**100**	**6**	**6**	**0.7618**	**0.00197**	**0.96574**	**0.73297**	**1.327**	**-**

The highest haplotype diversity is observed for ND2 (H = 0.7287) and D-loop (H = 0.7618). In contrast, 16S showed the lowest diversity (H = 0.2711). Tajima's D and Fu's F were largely non-significant across most markers, except for Paitan. Across all markers, the total nucleotide diversity (π) remained low (ranging from 0.0009 for 16S to 0.00232 for ND2), reflecting the generally low genetic variation in these populations.

The genetic variation results for the *C. porosus* population in Sabah, based on the analysis of the concatenated data, show a large number of haplotypes (19) among the 76 samples with sequence data for the four markers sequenced; however, the number of haplotypes per river was low with one or two haplotypes per river (Table 4.7). The 19 haplotypes were caused by 24 segregating sites, with the number of segregating sites per river ranging between one and two, except for the river Paitan that presented 14 segregating sites resulting in the formation of five haplotypes. This overall show that while there is a substantial amount of genetic diversity across the entire dataset, genetic variation is low within rivers. The summary statistics of genetic diversity (π and θ_W) were low, as expected from the low number of substitutions segregating in the rivers. The summary statistics sensitive to demographic changes (Tajima's D and Fu's F) were not significant indicating that the demographic history of *C. porosus* in Sabah seems to have been stable.

Table 4.7. Summary Statistics of Genetic Variation for Concatenated data. Number of individuals (n), number of haplotypes (nH), segregating sites (S), haplotype diversity (H), nucleotide diversity (π), Watterson's theta (θ_W), Tajima's D, Fu's F.

River	**n**	**nH**	**S**	**H (±SD)**	**π (±SD)**	**Θw (±SD)**	**Taj D**	**Fu's F**
Kinabatangan (KTS)	14	2	1	0.419	0.000185	0.308	0.742	0.909
Bengkoka (BGS)	8	2	1	0.286	0.00009	0.00013	-1.00623	-0.095
Kalumpang (KGS)	5	1	0	0.000	0.000	0.000	0.000	0.000
Klias (KLS)	7	3	2	0.667	0.000240	0.816	-0.275	-0.438
Padas (PDS)	3	1	0	0.000	0.000	0.000	0.000	0.000
Paitan (PTS)	7	5	14	0.9048	0.00219	2.828	1.699	0.936
Silabukan (SBS)	12	4	2	0.636	0.00031	0.310	1.356	-0.658
Serudong (SDS)	12	2	1	0.282	0.000120	0.322	-0.274	0.240
Segama (SGS)	8	3	2	0.200	0.000128	0.353	-1.112	-0.339
West Coast Rivers	10	3	2	0.6222	0.00029	0.000	0.8302	0.253
East Coast Rivers	66	16	20	0.8856	0.00109	0.001	-0.26824	-1.697
All Rivers (Concatenated)	76	19	24	0.9074	0.00231	0.00155	0.34236	-1.811

Analysing the data by individual rivers provides more refined insights. For instance, the Kinabatangan River, with 14 samples, exhibited very low genetic diversity with only two haplotypes and one segregating site, resulting in a haplotype diversity of 0.419 and a nucleotide diversity of 0.000185. In contrast, the Paitan River showed notable genetic variation with five haplotypes across 14 segregating sites in just seven samples, yielding a haplotype diversity of 0.9048 and a much higher nucleotide diversity of 0.00219. Watterson's theta for Paitan was 2.828, and both Tajima's D (1.699) and Fu's F (0.936).

When comparing the east coast and west coast river populations, distinct differences emerge. The east coast rivers, with 66 samples, exhibited 16 haplotypes and 20 segregating sites, resulting in a haplotype diversity of 0.8856 and a nucleotide diversity of 0.00109. The West Coast rivers, with 10 samples, presented only three haplotypes and two segregating sites, leading to a haplotype diversity of 0.6222 and a nucleotide diversity of 0.00029. However, a comparison between the two coasts for the number of haplotypes and segregating sites, conditioning for sample size, resulted in no significant differences between them (chi square p-value > 0.05). Tajima's D and Fu's F values for the east coast were -0.26824 and -1.697, respectively, whereas the west coast values were 0.8302 (Tajima's D) and 0.253 (Fu's F).

The haplotype map of *C. porosus* populations across all rivers in Sabah provides a comprehensive overview of the genetic diversity and distribution of this species in the region (Figure 4.2). It shows considerable differences in haplotype composition between the West and East Coast populations. Firstly, the three haplotypes found in Klias River and Padas River are unique to this region and are not present in the East Coast rivers. The West Coast rivers also show limited genetic diversity compared to the East Coast rivers. In Klias River (n=7), there are three haplotypes represented, with Hap 6 being the most dominant, followed by minor contributions from Hap 5 and Hap 7. Padas River (n=3) exhibits an even more constrained genetic diversity with only a single haplotype present (Hap 6).

In contrast, the East Coast rivers exhibit a higher degree of haplotype diversity. Bengkoka River (n=7), Kinabatangan River (n=14) and Serudong River (n=12) each have two haplotypes. Paitan River (n=7) stands out with five haplotypes, suggesting a complex population structure with significant genetic mixing and historical events influencing its diversity. Similarly, Silabukan River (n=12) with four haplotypes and Segama River (n=8) with three haplotypes indicate considerable genetic variability. Kalumpang River (n=5) shows limited diversity with only one haplotype present.

The clear-cut difference in haplotype distribution between the West and East Coast rivers highlights the diverse evolutionary pressures and historical events that may have shaped these populations. The East Coast rivers, with their greater haplotype diversity, suggest larger, more interconnected populations that have experienced less isolation and more gene flow, possibly due to geographic or ecological factors that facilitate movement and mixing. In contrast, the West Coast populations appear more isolated with reduced genetic diversity, which could be due to geographic barriers, smaller population sizes, or historical bottlenecks limiting genetic exchange.

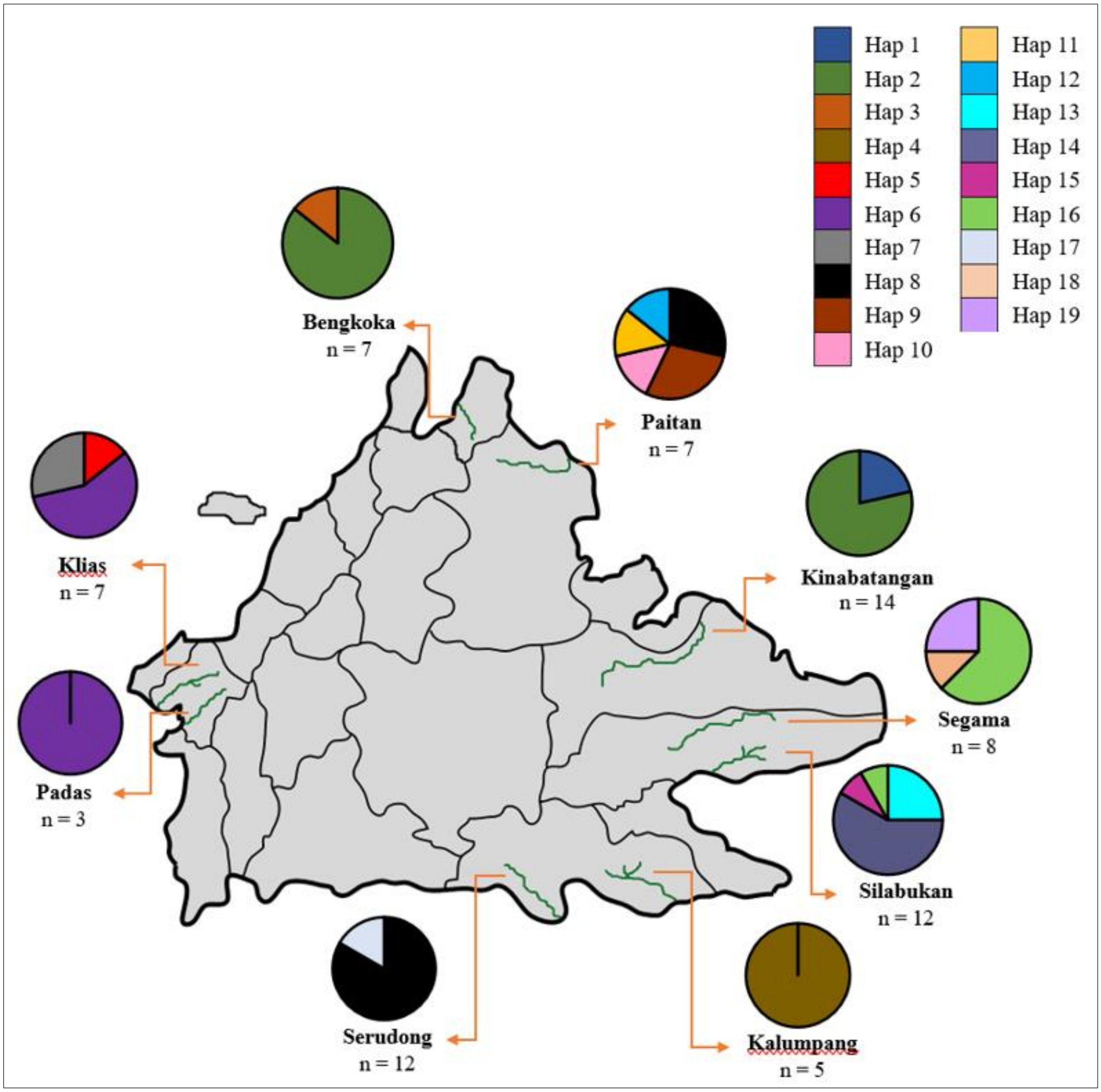


Figure 4.2. Map of Sabah and corresponding pie charts of haplotypes present in each river. Black lines show district boundaries. Green lines indicate rivers: Bengkoka (BGS), Paitan (PTS), Kinabatangan (KTS), Segama (SGS), Silabukan (SBS), Kalumpang (KGS), Serudong (SDS), Padas (PDS), and Klias (KLS) and n = no. of individuals sampled from that river. Each haplotype (hap) is represented by a different colour.

The haplotype network illustrates the genetic relationships and diversity among the nine riverine subpopulations (Figure 4.3). Each circle represents a distinct haplotype, with the size of the circle proportional to the frequency of that haplotype in the population. The colours within the circles correspond to different rivers, as indicated in the legend.

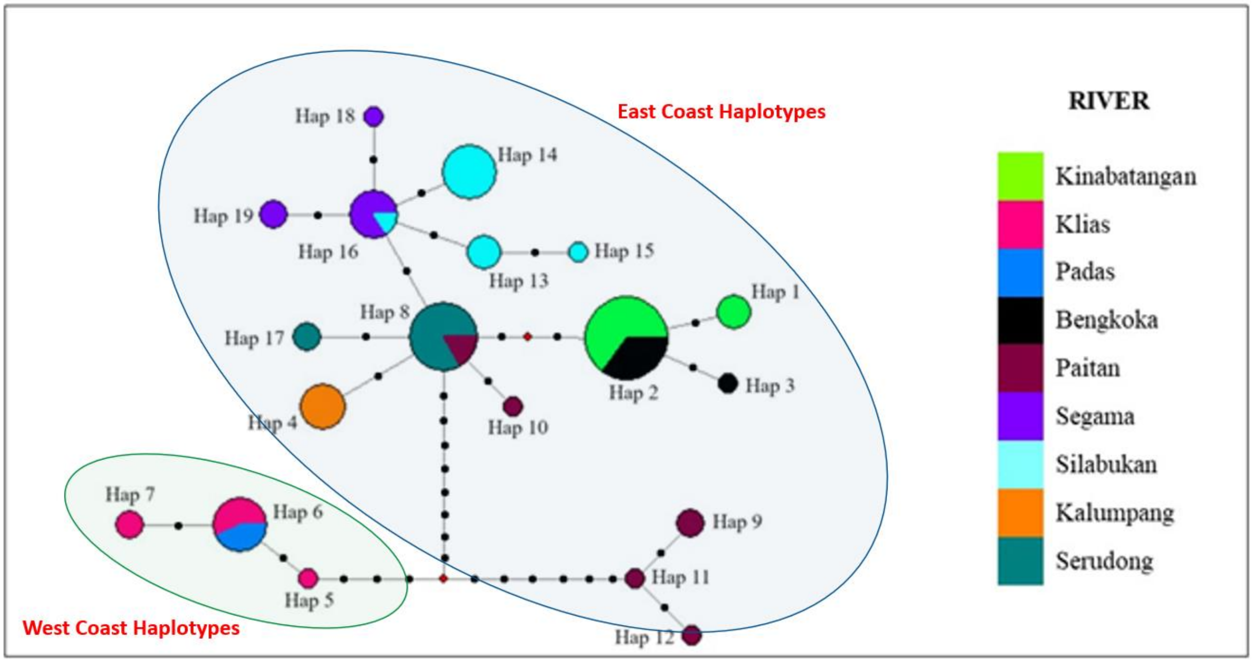


Figure 4.3. Neighbour joining haplotype network of *C. porosus* mtDNA region. Area of each circle is proportional to haplotype frequency. Dots indicate the number of mutations between haplotype sequences

The East Coast haplotypes are clustered within a larger group, with the most frequent haplotype (Hap 2, Hap 8, Hap 16) shared among multiple rivers. The remaining haplotypes in the East Coast are specific to particular rivers, reflecting localized genetic structuring. Conversely, the West Coast haplotypes form a distinct cluster with Hap 6 shared between Klias and Padas. Hap 5 and Hap 7 are unique to Klias. The network shows no overlap between the east and west coast haplotypes, indicating a lack of shared genetic connectivity between these regions. Haplotype networks were also generated for each of the markers individually (Appendix I-IV).

Population Structure

The AMOVA results for the *C. porosus* population in Sabah reveal significant genetic differentiation among groups (East Coast and West Coast) and populations in the groups, and within populations (Table 4.8).

Table 4.8. AMOVA summary of the *C. porosus* population in Sabah

Source of Variation	d.f	Sum of squares	Variance components	Percentage of variation	p-values
Among groups	1	94.537	4.91167 Va	71.40	0.02835+-0.00561
Among populations within groups	7	84.729	1.34374 Vb	19.53	0.000
Within populations	67	41.786	0.62367 Vc	9.01	0.000
Total	75	221.053	6.87907	-	
Fixation index F_{ST}	0.90934				

The analysis indicates that 71.40% of the total genetic variation is attributed to differences among the East Coast populations and the West Coast populations, with a variance component (Va) of 4.91167. This high percentage of variation among populations, combined with a significant p-value of 0.02835, suggests strong genetic structuring and limited gene flow between the *C. porosus* populations of the East and West Coast. The fixation index (F_{ST}) of 0.90934 further supports this conclusion, indicating a high level of genetic differentiation. In contrast, 9.01% of the genetic variation is found within populations, with a variance component (Vc) of 0.62367. Although this within-population variation is significant (p-value of 0.000), it is substantially lower than the variation observed among populations.

The pairwise F_{ST} values for *C. porosus* populations across the nine rivers in Sabah indicate varying levels of genetic differentiation between populations and between the East and West Coast populations (Table 4.9).

Table 4.9. Pairwise F_{ST} for *C. porosus* populations across nine rivers in Sabah. F_{ST} values are shown below the diagonal and FDR corrected p-values are shown above the diagonal. The pairwise comparison West/East does not have its p-value corrected.

FDR corrected threshold for significance is 0.01197731248 for all except East and West Ccoast

River	**KTS**	**BGS**	**KGS**	**PTS**	**SBS**	**SDS**	**SGS**	**KLS**	**PDS**	**EAST**	**WEST**
KTS		0.42342	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000		
BGS	0.08184		0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000		
KGS	0.91560	0.89770		0.01802	0.00000	0.00000	0.00000	0.00000	0.00901		
PTS	0.70057	0.61736	0.50643		0.00000	0.00901	0.00000	0.00000	0.03604		
SBS	0.84715	0.82035	0.61196	0.63174		0.00000	0.00000	0.00000	0.00000		
SDS	0.85494	0.83546	0.81763	0.59571	0.70629		0.00000	0.00000	0.00901		
SGS	0.78966	0.74026	0.82301	0.58342	0.53935	0.74507		0.00000	0.00000		
KLS	0.95776	0.94314	0.95084	0.58442	0.92724	0.95164	0.93034		0.14414		
PDS	0.97802	0.96954	1.00000	0.51203	0.94224	0.97904	0.95285	0.21959			
EAST											0.00000
WEST										0.75764	

The FST values observed ranged from 0.8184 (Bengkoka vs. Kinabatangan) to 0.97802 (Padas vs. Kalumpang). Populations within the same geographic region exhibited relatively lower FST values, with an average FST of 0.6906 for East Coast populations and 0.21959 for West Coast populations. In contrast, comparisons between East Coast and West Coast populations yielded a significantly higher average FST of 0.75764 (t = 3.699104, p = 0.00076).

Demographic History

The mismatch distribution of the *C. porosus* population (Figure 4.4) at the state-wide level shows a bimodal distribution, indicated by two distinct peaks in the observed pairwise differences (red line). This pattern contrasts with the expected distribution under a demographic expansion model (blue dotted line). The first peak, occurring at low pairwise differences, reflects a high frequency of closely related haplotypes, while the second peak at higher pairwise differences suggest a subset of haplotypes with greater genetic divergence. The observed deviations from the expected distribution indicate a non-uniform distribution of pairwise differences within the state-wide population.

At the regional level, the mismatch distribution for the West Coast population reveals a unimodal distribution, with a single peak at low pairwise differences. This closely follows the expected distribution under a demographic expansion model, indicating a more homogenous population with closely related haplotypes. In contrast, the East Coast population displays a bimodal distribution, with one prominent peak at low pairwise differences and a smaller peak at higher pairwise differences. This pattern suggests the presence of two distinct groups of haplotypes within the East Coast population. Both regional graphs exhibit differences in their mismatch patterns.

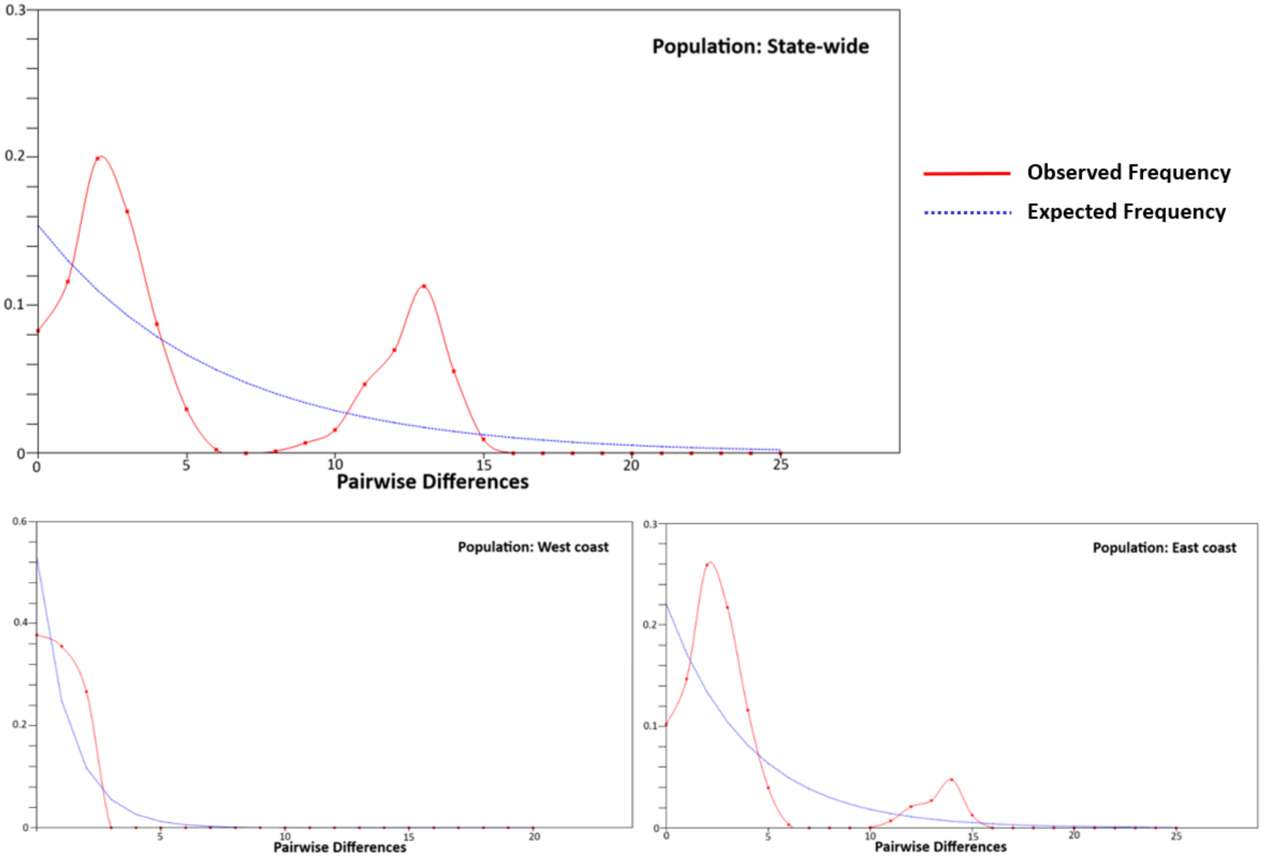


Figure 4.4 Mismatch distribution graph of the *C. porosus* state-wide population, West Coast population and East Coast population. Axis-x: pairwise differences, Axis-y: frequency of pairwise comparisons, green dotted line: expected frequency under a hypothesis of population expansion, red line: frequency observed.

To gain a more detailed perspective of the demographic patterns within each population, mismatch distribution analyses were conducted separately for the individual populations across the regions (Figure 4.5). The graphs illustrate varying patterns of pairwise differences across the populations. The populations from Padas and Kalumpang indicated an error due to the presence of a single haplotype in each river. Thus, the graphs for these populations were not plotted. The populations from Bengkoka, Kinabatangan, Segama, Serudong and Klias display unimodal distributions, with a single peak at low pairwise differences, closely matching the expected distribution under a demographic expansion model. This suggests that these populations are genetically homogenous, with low levels of genetic divergence among haplotypes.

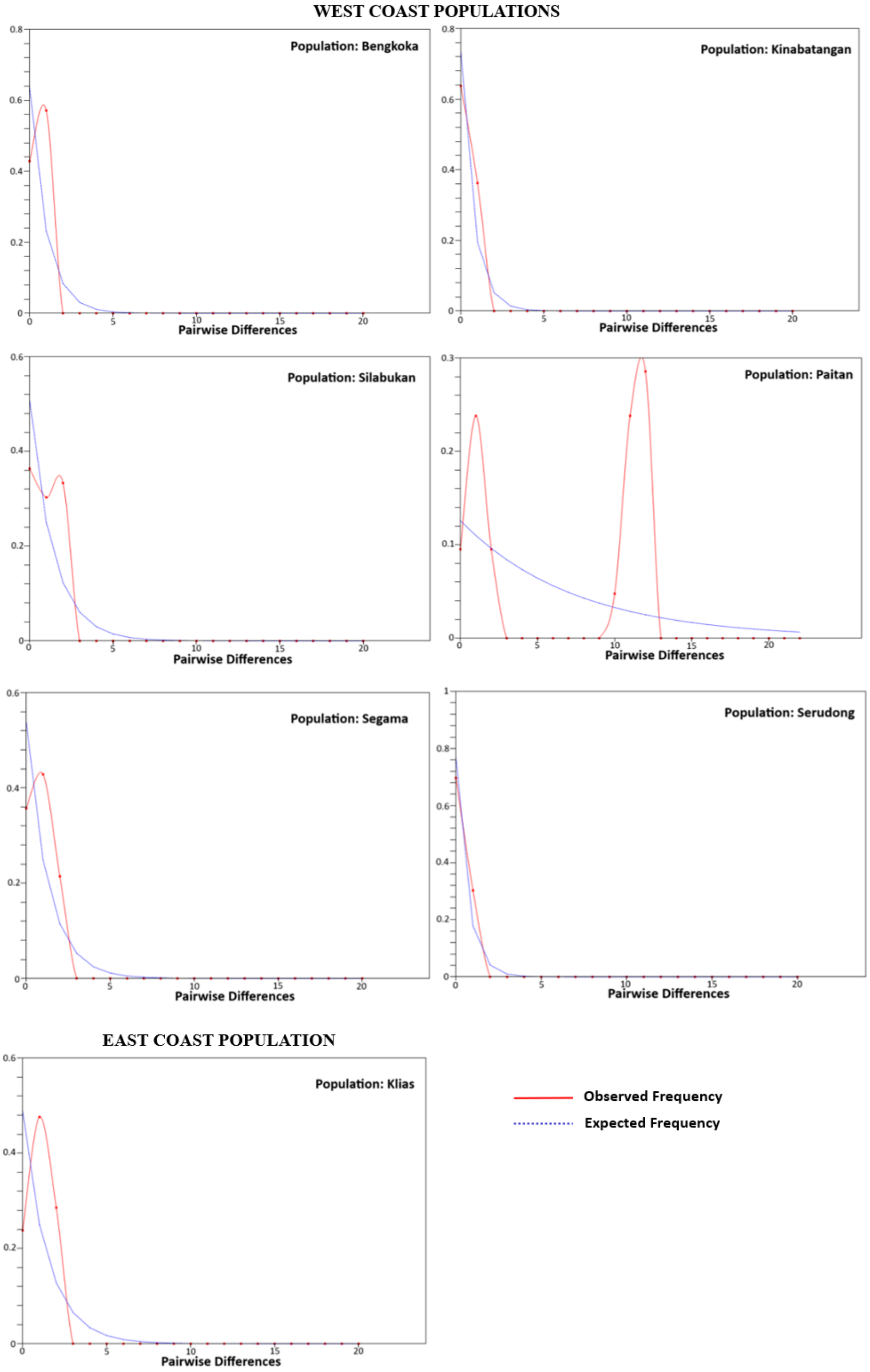


Figure 4.5 Mismatch distribution graph of *C. porosus* populations in six rivers. Axis-x: pairwise differences, Axis-y: frequency of pairwise comparisons, green dotted line: expected frequency under a hypothesis of population expansion, red line: frequency observed.

In contrast, the population of Paitan shows a clear bimodal pattern with a secondary peak at higher pairwise differences. Similarly, Silabukan's observed distribution shows slight deviation from the expected curve, with peaks at both low and moderate pairwise differences. The mismatch distribution was also plotted for the east coast population with the removal of Paitan and it displays a unimodal distribution similar to the remaining rivers (Appendix V). The demographic analysis using the mismatch distribution was complemented by Bayesian Skyline Plot (BSP) reconstructions. The BSP analyses were limited to the full dataset (all samples and all markers), all markers analysed separately for the East and West Coast datasets (Figure 4.6), and all samples for each marker separately (Figure 4.7).

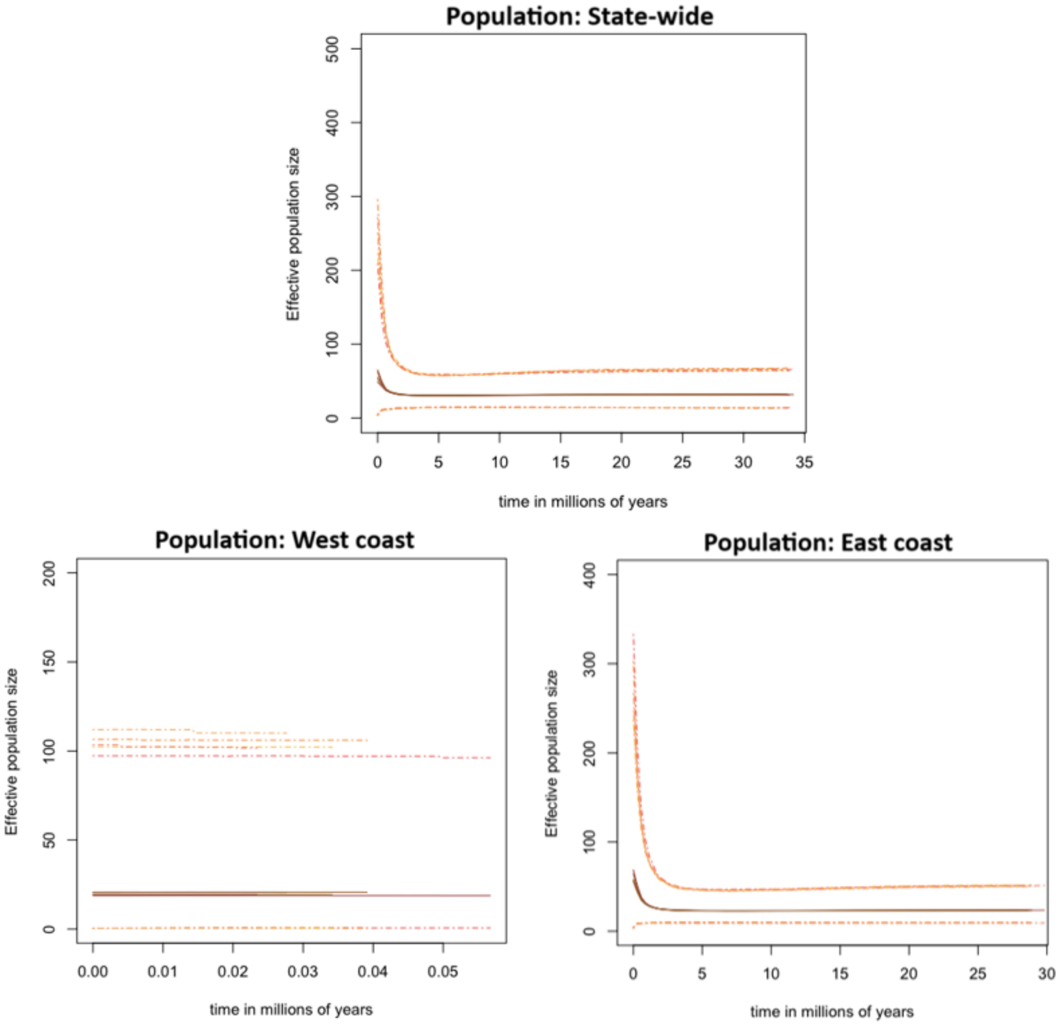


Figure 4.6. Bayesian Skyplot reconstruction of state-wide population, east coast population and west coast population.

Full dataset resulted in a largely stable demography through most of the past, however, with a likely population expansion occurring within the last million years. The analysis of all samples for each separate marker resulted in similar patterns indicative of a population expansion in Sabah's *C. porosus* relatively recent history. The split of the dataset into the East and West coasts resulted, however, in a contrasting demographic history inference. While for the West Coast no population expansion was determined during their recent history, the East coast indicated a population expansion in their recent history.

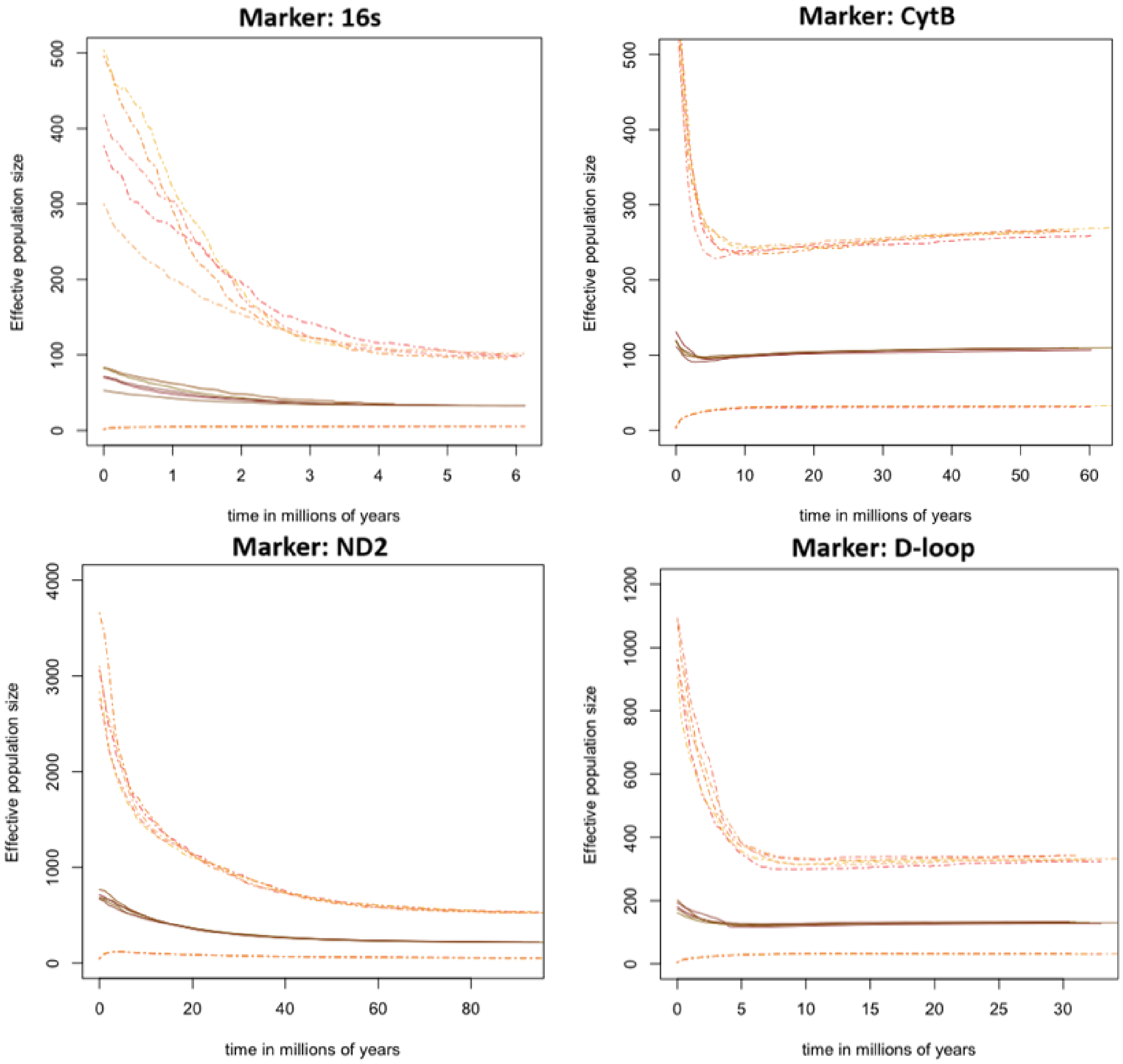


Figure 4.7 Bayesian Skyplot reconstruction of all four markers.

Phylogeny

The maximum likelihood tree for the *C. porosus* population in Sabah provides a detailed view of the genetic relationships and evolutionary history of these populations (Figure 4.8). The best models of DNA sequence evolution identify by iQtree were HKY + F + I for ND2 and HKY + F for 16S, CytB and D-Loop; F stands for empirical base frequencies assuming unequal base frequencies and I indicates that a range of positions in the alignment were invariable (i.e. had no polymorphisms).

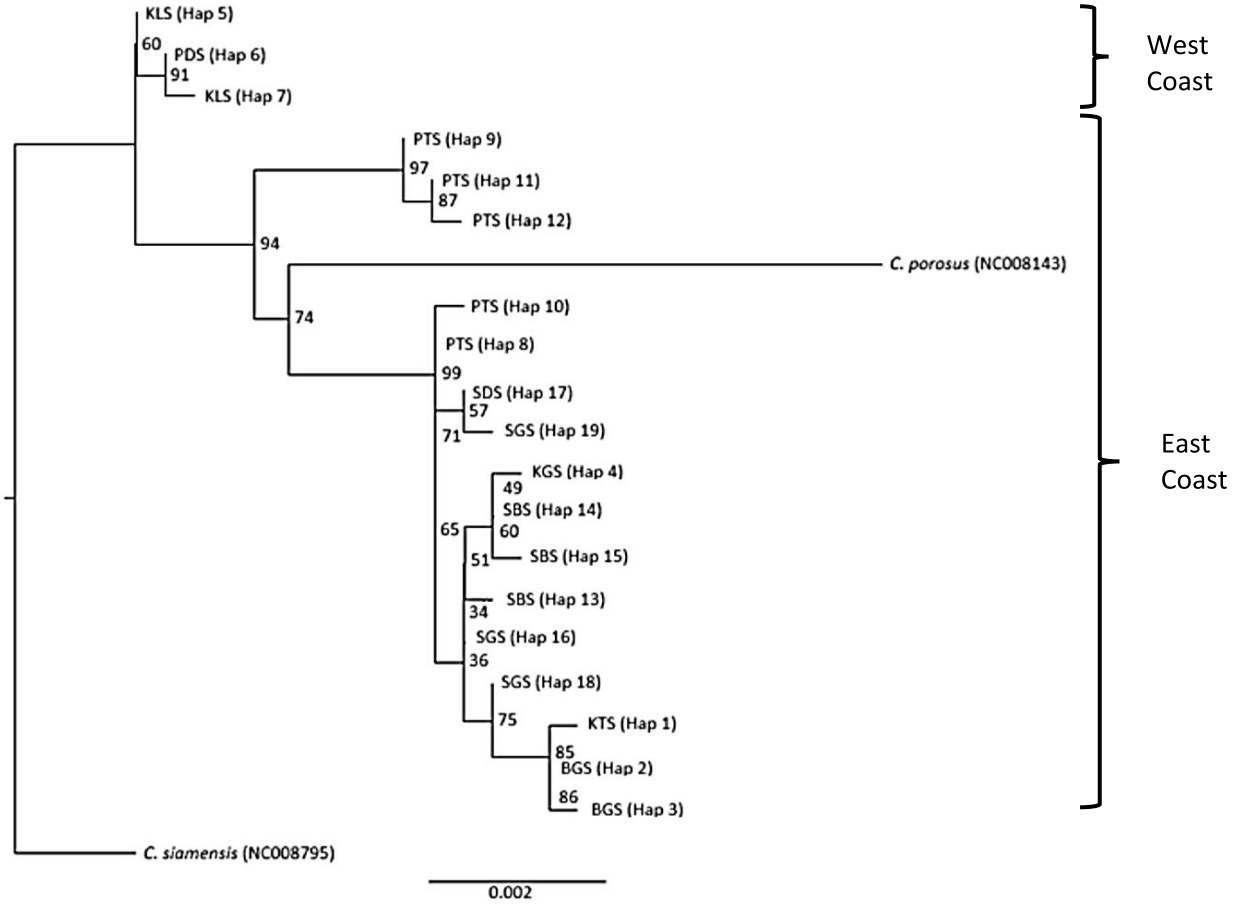


Figure 4.8. Maximum likelihood (ML) phylogenetic tree.

The phylogenetic tree shows the relationships among the haplotypes of *C. porosus* populations from Sabah, with *C. porosus* (NC008143) and *C. siamensis* (NC008795) included as outgroup references. Haplotypes 5, 6, and 7, representing the West Coast population, cluster together with a bootstrap support of 60. In contrast, the remaining haplotypes, which form the East Coast population, are distributed across several clades with varying levels of bootstrap support. Haplotypes 1, 2, and 3 cluster together and exhibit a close relationship, while haplotypes from Paitan (Hap 9, 11, 12) form a separate, well-supported clade. The two outgroup samples are clearly separated from the Sabah haplotypes, with *C. porosus* (NC008143) being more closely related to the Sabah samples, consistent with its designation as the reference sequence for this species. *C. siamensis* (NC008795) is more distantly placed on a separate branch, reflecting its status as a different species.

4.4 Discussion

The results of this chapter represent the first comprehensive analysis of genetic structure in the *C. porosus* population in Sabah. Although a previous genetic study was carried out some eight years ago, it was focused solely on the *C. porosus* population in the Kinabatangan River (Evans, 2016 Chapter 6). This study, involving nine major riverine populations, provide new and significant information to understand the evolutionary history and genetic partitioning patterns of this species.

Mitochondrial DNA (mtDNA) is one of the most commonly used genetic markers in animal population studies. Its widespread application is attributed to its high variability, maternal (clonal) mode of inheritance, and the ability to link mtDNA diversity with demographic factors, such as changes in population size across species or populations. These characteristics make mtDNA a dependable tool for biological conservation research (Harrison, 1989; Roman & Palumbi, 2003; Nabholz *et al*., 2008).

As mentioned earlier in the methodology section, the genetic analysis in this chapter primarily utilized concatenated data, which included joint sequences from four genetic markers, which represent four domains/regions (16S, CytB, ND2 and D-loop) of the mitochondrial DNA. To ensure consistency and completeness, only samples with full nucleotide sequences across all markers were retained in the concatenated dataset. Samples that lacked sequence data for any of the markers were excluded. Concatenating data in this way is a common approach in phylogenetic studies to enhance resolution and robustness, as it leverages combined information from multiple markers (Lecocq *et al.,* 2013; Wiens, 1998).

Genetic Variation

The genetic variation observed in *C. porosus* populations in Sabah highlights interesting patterns of diversity, with 19 haplotypes and 24 segregating sites identified among 76 samples sequenced for 3175 base pairs of the mitochondrial genome. When compared to previous studies, the current findings reflect a higher level of haplotype diversity (H = 0.9071). For instance, a study conducted on *C. porosus* populations in the Northern Territory of Australia by Luck *et al*. (2012) reported only three haplotypes among 61 samples, and a haplotype diversity, H of 0.4. Similarly, Russello *et al*. (2006) investigated *C. porosus* populations in Palau and identified just one haplotype across 39 samples, with a haplotype diversity, H of 0.00. Both these studies focused on a single mitochondrial domain, which may have contributed to the lower genetic variation observed.

The study by Luck *et al*. (2012) utilized the mitochondrial 12S rRNA domain, which has been associated with low levels of genetic diversity in other crocodilian species as well. For example, comparative studies on *C. acutus* and *C. niloticus* populations also showed low haplotype diversity when analysed using the 12S marker. This is consistent with the general observation that the 12S domain may not be as variable as other mitochondrial regions, thus limiting its capacity to detect high levels of genetic divergence. Russello *et al*. (2006), on the other hand, did not specify the domain used in their study, but their reliance on a single domain as well might explain the limited variation observed in their results.

Studies have reported that *C. porosus* exhibits relatively low mitochondrial DNA (mtDNA) diversity compared to other crocodilian species. For instance, research analysing *C. porosus* populations in Australia's Northern Territory identified limited mtDNA variation, with a predominant haplotype shared across multiple river basins. This is in contrast with findings in *C.*

niloticus, which displayed higher levels of genetic variation across different regions (Asch *et al*., 2019). In the study from the Northern Territory of Australia, the low mtDNA diversity was attributed to historical demographic events. It was suggested that a rapid population contraction due to intensive hunting before the 1970s reduced mtDNA diversity. During the subsequent recovery period, the small number of remaining mtDNA haplotypes became fixed as the population rebounded over the last 50 years or so (Fitzsimmons *et al*., 2002).

Venegas-Anaya *et al*. (2008) on the other hand, investigated *Caiman crocodilus* populations across Mesoamerica and South America using combined mitochondrial markers - Cytochrome b and Cytochrome c oxidase subunit I (COI). This approach revealed higher genetic divergence and greater resolution of haplotypes compared to studies relying on single domains. Another study using combined markers on *C. niloticus* populations in southern Africa revealed a high haplotype diversity of 0.861, with a total of 16 haplotypes across 133 samples (Van Asch *et al*., 2019).

The current study, which employed four mitochondrial domains (ND2, 16S, Cytb, and D-loop), provides a more comprehensive view of genetic variation in *C. porosus* populations. The multi-marker approach in mtDNA studies is instrumental in capturing a broader spectrum of genetic variation, as different mtDNA regions evolve at varying rates, thereby revealing distinct aspects of population genetics. This idea is supported by research indicating that the mitochondrial control region, often referred to as the D-loop, exhibits a higher mutation rate compared to coding regions, making it particularly useful for analysing recent evolutionary events and population dynamics. In contrast, mtDNA coding regions, such as CytB, 16S and ND2, which evolve more slowly due to functional constraints, are valuable for investigating deeper phylogenetic relationships and long-term evolutionary processes. By combining data from both rapidly and slowly evolving regions, researchers can achieve a more comprehensive understanding of genetic diversity and evolutionary history within and among populations (Meyer & Zardoya, 1999). These findings underscore the importance of selecting appropriate markers and in this case, mitochondrial regions for accurately assessing genetic diversity.

On the other hand, a study by Unajak *et al.* (2017) analysed the genetic diversity of captive *C. porosus* populations in Thailand. The researchers found that the captive populations maintained a high level of haplotype diversity (0.924), which was attributed to the diverse genetic backgrounds of the founder individuals and effective management practices aimed at preserving genetic variation. The study emphasized the importance of genetic monitoring and management in captive breeding programs to ensure the maintenance of genetic diversity. Another study on the critically endangered *C. intermedius* in Colombia revealed that the largest captive-bred population preserved much of its founder diversity and showed no signs of inbreeding, making it suitable for implementing wild releases (Saldarriaga-Gómez *et al*., 2023).

However, it is important to note that while some captive populations may retain or even exhibit higher genetic diversity compared to certain wild populations, and may seem like a good alternative for preserving genetic integrity, this is not always the case. Captive populations are susceptible to genetic drift, inbreeding, and adaptation to captivity, which can reduce genetic diversity over time (Shcenekar & Weiss, 2016). Therefore, careful genetic management is crucial to maintain or enhance genetic diversity in captive breeding programs.

Moving forward, the genetic structure of the *C. porosus* population in Sabah shows low haplotype diversity within individual rivers (typically one or two per river), with the exception of Paitan, Klias and Silabukan Rivers, suggesting that genetic variation is unevenly distributed and highly localized. This pattern could reflect limited gene flow between rivers, likely due to geographic or ecological barriers that restrict the movement of individuals and, consequently, the exchange of genetic material. Such localized patterns of genetic variation may also result from founder effects or the influence of small effective population sizes within rivers (Allendorf, 2017).

The Paitan River exhibited the highest levels of genetic diversity among all surveyed rivers, with the highest haplotype diversity ($H = 0.9048$) and nucleotide diversity ($\pi = 0.0021$), indicating a substantial amount of genetic variation within this population alone. Additionally, Paitan had the most segregating sites ($S = 14$), further supporting the presence of multiple unique genetic lineages within the population. Interestingly, one of the haplogroups in Paitan appears to lie between the East and West haplogroups of Sabah, suggesting the possibility of immigration from an external population not included in this study. This unique positioning raises questions about potential historical or occasional gene flow from an unidentified source population. The high values for summary statistics of genetic variation in the Paitan population suggest that this river supports a stable and well-connected population, with ample gene flow allowing for a wide range of genetic variation (Tajima, 1989). The combination of high haplotype diversity and numerous segregating sites implies that this population has likely not experienced recent bottlenecks or severe reductions in size, which would typically reduce genetic diversity. While segregating sites capture genetic differences at individual positions, haplotypes offer a higher-order perspective on how these variations group together to form unique genetic lineages (Nei & Kumar, 2000).

The Klias River and the Silabukan River had haplotype diversities, H of 0.667 and 0.636 respectively. Klias River traverses the Klias Wetlands which is a mangrove forest reserve rich in biodiversity. This area supports a variety of wildlife, including proboscis monkeys, macaques, and numerous bird species. The Silabukan River on the other hand flows through the Silabukan Protection Forest Reserve which encompasses a range of ecosystems, including lowland dipterocarp forests and freshwater swamps, providing suitable habitats for diverse wildlife. In both regions, the presence of diverse and intact habitats possibly facilitates gene flow that help maintain genetic diversity within *C. porosus* populations.

The Padas River and the Kalumpang River both displayed low genetic diversity, with only one haplotype (H = 0.00) observed in each population. The low haplotype diversity in Padas River could partially be attributed to the small sample size (n = 3), which may not fully capture the genetic variation within this population. Additionally, although the Padas River is situated in close proximity to the Klias River, both rivers have distinct drainage systems and do not intersect, which likely limits opportunities for gene flow between their respective *C. porosus* populations.

In the case that Padas and Klias Rivers were hydrologically connected, there would be a greater potential of gene flow between the crocodile populations inhabiting these waterways. Hydrological connectivity between river systems increases the likelihood of higher genetic variation in aquatic animals by facilitating gene flow and reducing population isolation. For instance, Hughes *et al*. (2009) noted that connected river networks promote genetic exchange among populations of aquatic species, leading to greater genetic diversity within interconnected systems compared to isolated ones. Similarly, Cegelski *et al*. (2006) emphasized the importance of hydrological connectivity in maintaining genetic diversity in aquatic species by enabling the dispersal of individuals and preventing genetic drift. However, the separation of the Klias and Padas drainage systems creates distinct population structures, as individuals are unlikely to traverse between the rivers, thereby restricting gene flow and contributing to the observed low haplotype diversity in the Padas River population.

Similarly, a study on *C. porosus* populations in Queensland, Australia, demonstrated that geographically close sub-populations showed evidence of both historical and recent movement, with gene flow declining as geographic distance increased. The study highlighted that genetic connectivity was greater along the Western Cape and Gulf regions, with more genetic differentiation compared to the east coast, where restricted gene flow was observed (Queensland Department of Environment and Science, 2018), further emphasizing the critical role of hydrological connectivity in maintaining genetic diversity in aquatic species.

As such, isolated river systems, like Padas and Klias Rivers, are more likely to experience genetic drift, founder effects, and reduced genetic exchange, ultimately leading to localized genetic bottlenecks. The observed low diversity in Padas River also emphasizes the need for larger sample sizes to verify these results and further explore the impacts of geographic separation on genetic variation in this population.

Similarly, the Kalumpang River, which exhibited low genetic diversity, also had a small sample size (n = 5). However, when compared to the Paitan River, which also had a small sample size (n = 7) but demonstrated high genetic diversity, it becomes evident that sample size alone does not dictate genetic diversity. Factors such as limited gene flow, inbreeding, and population history likely play a significant role in shaping the genetic structure of these populations.

The genetic diversity of the Kinabatangan population ($H = 0.419$, $\pi = 0.000185$) ranked only as the fourth highest among all rivers analysed, even with the largest sample size (n = 14) of all populations. Given its ecological importance and status as home to one of Sabah's largest crocodile populations (as highlighted in Chapter 3), it would be reasonable to assume that the *C. porosus* population in this river would exhibit high genetic diversity. However, the observed haplotype diversity again suggests other factors may be influencing the genetic variation.

One potential limiting factor could be the historical or contemporary barriers to gene flow along the river. While the Kinabatangan River is extensive, human-made structures such as bridges and habitat fragmentation could restrict movement and reduce genetic mixing among sub-populations within the river. Chapter 3 noted that five crocodiles tracked in this river moved near a man-made overhead bridge but never crossed past under it, indicating a potential behavioural or physical barrier to dispersal. Additionally, historical bottlenecks or founder effects may have reduced genetic variation in the population, with subsequent recovery being constrained by limited genetic influx.

Furthermore, the Kinabatangan River is subject to environmental pressures, including deforestation and habitat modification for agricultural expansion, particularly oil palm plantations. These activities could fragment habitats and create isolated sub-populations, limiting opportunities for gene flow and reducing genetic diversity over time. Although the genetic diversity in the Kinabatangan population is still moderately high, these factors likely contribute to its lower-than-expected genetic variation, emphasizing the importance of preserving connectivity and habitat integrity to sustain genetic diversity.

Among the 19 haplotypes identified in this study, 15 are unique to specific populations, while only four haplotypes are shared between populations. The distribution of these unique haplotypes varies across rivers. The Paitan River stands out with four unique haplotypes (Hap 8, Hap 9, Hap 10, Hap 11) out of the five identified, the highest among all populations. The Silabukan River also shows high genetic uniqueness, with three of its four haplotypes (Hap 13, Hap 14, Hap 15) being unique. Klias and Segama Rivers follow, each with two unique haplotypes (Hap 5, Hap 7 and Hap 18, Hap 19, respectively). Meanwhile, Serudong, Kalumpang, Kinabatangan, and Bengkoka Rivers each have one unique haplotype (Hap 17, Hap 4, Hap 1, Hap 3, respectively). Despite being the largest river with the largest sample size, Kinabatangan's population exhibits surprisingly low genetic uniqueness, with just one unique haplotype, while populations like Paitan and Silabukan exhibit remarkable differentiation.

Conversely, the four shared haplotypes reflect some degree of gene flow between certain populations. In most cases, shared haplotypes are likely to be observed among geographically proximate rivers with fewer physical or ecological barriers. For example, Hap 6 was shared between the neighbouring rivers Padas and Klias, while Hap 16 was shared between the neighbouring rivers Segama and Silabukan, suggesting some level of genetic exchange facilitated by their proximity. In contrast to this pattern, Hap 2 and Hap 8 were shared between rivers that are geographically distant from each other. Hap 2 was shared between Bengkoka and Kinabatangan, while Hap 8 was shared between Paitan and Serudong. These distant shared haplotypes may reflect rare long-distance dispersal events in the past that have allowed for some level of genetic exchange despite their spatial separation.

The haplotype patterns observed in the Padas and Klias Rivers, as well as the Segama and Silabukan Rivers, suggest a combination of historical connectivity and current genetic isolation. Padas and Klias share one haplotype (Hap 6), while Klias retains two unique haplotypes not found in Padas. Similarly, Segama and Silabukan share one haplotype (Hap 16), but the remaining haplotypes are unique to each river. The shared haplotypes between neighbouring rivers indicate that these populations likely had historical or recent gene flow, potentially when the rivers were hydrologically connected, or through movement facilitated by seasonal flooding or coastal dispersal. However, the emergence of unique haplotypes in each river suggests that they are now largely isolated, possibly due to changes in hydrology, environmental shifts, or human activities that have disrupted connectivity. Additionally, although these rivers flow into the same coastal waters, *C. porosus*, which is capable of long-distance coastal travel, may no longer use these coastal areas as a dispersal route as frequently. This could result from behavioural changes, ecological pressures, or anthropogenic factors that discourage movement across the coastline, leading to genetic isolation.

Coastal areas, which once served as important dispersal corridors for species such as *C. porosus*, may now be less frequently utilized due to a combination of behavioural shifts, ecological changes, and human-induced pressures. Coastal development, such as the construction of ports, marinas, and urban settlements, often leads to habitat fragmentation and pollution, which can alter the suitability of these habitats for crocodile movement. For example, studies have documented the impact of urbanization on coastal ecosystems, with increased boat traffic and fishing activities deterring wildlife from utilizing these areas for migration or dispersal (Hays *et. al*., 2016). In the case of *C. porosus*, disturbances such as noise pollution, habitat modification, and reduced prey availability in coastal zones may contribute to avoidance behaviours, leading to restricted gene flow between riverine populations.

Anthropogenic pressures, such as illegal hunting and human-wildlife conflicts, can significantly impede the movement of species in coastal areas. Similar trends have been observed in other aquatic species, where coastal industrialization and fishing activities disrupt migratory corridors. For instance, industrial fishing poses substantial threats to marine predators, including turtles and sharks, by increasing the risk of bycatch and habitat degradation (Dulvy *et al*., 2014; Civil Beat, 2024). Additionally, coastal development and human activities have been shown to impact commercially important fish and invertebrate species by degrading essential habitats used for spawning, juvenile growth, and migration (Brown *et al*., 2018). These disruptions can lead to reduced genetic diversity and hinder the natural movement patterns of these species.

However, long-distance movements via coastal migration could have occurred in the past when coastal habitats were less fragmented and human activity less pronounced. *C. porosus* is known for its ability to traverse long distances across open seas. For example, Campbell *et al.* (2010) observed a male *C. porosus* traveling over 400 km from the Kennedy River in Queensland, Australia, to the Wenlock River. Additionally, Grigg & Kirshner (2015) noted that individuals can travel distances exceeding 800 km, highlighting their remarkable dispersal ability via marine environments. Some coastlines in Sabah could have once served as a corridor for individuals moving between rivers. Shared haplotypes among geographically distant populations may therefore represent a relic of historical connectivity between some populations. FitzSimmons *et al.* (2001) found shared haplotypes in *C. johnstoni* populations across distant river systems, suggesting past connectivity via hydrological or marine corridors. This pattern can also apply to

C. porosus, where shared haplotypes could reflect historical gene flow before the fragmentation of coastal habitats.

Another research on *C. acutus* has revealed notable genetic relationships between populations in Cuba and Jamaica. This study found that individuals from these islands share certain haplotypes, indicating historical gene flow between these geographically separated populations (Rossi *et al.*, 2020) suggesting that despite the physical distance, there was movement of individuals across marine environments, facilitating genetic exchange.

The general predominance of unique haplotypes suggests a high degree of genetic differentiation and supports the theory of limited gene flow among the populations inhabiting different rivers. It reflects the independent evolutionary trajectory of a population and may be indicative of localized adaptation to specific environmental conditions (Avise, 2000). On the other hand, the sharing of haplotypes could indicate connectivity among populations, allowing the exchange of genetic material through movement and interbreeding. This pattern may be observed in populations within close proximity or those connected by corridors such as waterways or floodplains. Alternatively, shared haplotypes may also reflect ancestral polymorphisms retained across populations due to incomplete lineage sorting (Templeton *et al*., 1992). However, the limited number of shared haplotypes compared to unique ones underscores that such exchanges are relatively rare or have been disrupted over time.

The haplotype network reveals a clear division between the West Coast and East Coast populations of *C. porosus* in Sabah, with distinct haplotypes largely confined to their respective geographic regions. The West Coast populations are represented exclusively by Hap 5, Hap 6, and Hap 7, and these haplotypes are not found in the East Coast populations. In contrast, the remaining 16 haplotypes are restricted to the East Coast populations. This suggests the presence of two genetically differentiated subpopulations within the Sabah *C. porosus* population. The absence of shared haplotypes between these regions points to limited or no contemporary gene flow between the two groups.

The genetic separation between the East and West Coast haplotypes is further emphasized by the number of mutations separating these groups. The haplotypes in both coasts are separated by at least 12 mutations, a considerable genetic distance that supports the hypothesis of long-term isolation between these subpopulations. Within the east coast populations however, the Paitan population exhibits even greater divergence. Haplotypes 9, 11, and 12, which are unique to Paitan, are separated by as many as 15 mutations from the next closest East Coast haplotype (Hap 8). This striking level of divergence within the East Coast suggests that the Paitan population has experienced unique evolutionary pressures or long-term isolation from other East Coast populations.

The presence of distinct genetic clusters and substantial mutational differences between haplotypes is crucial for understanding the population structure and evolutionary history of *C. porosus* in Sabah. These findings suggest that geographic features, such as the Crocker Range, may act as indirect barriers by shaping the hydrological systems and river networks, thereby limiting gene flow between populations on the east and west coasts. Rather than suggesting direct overland dispersal, the genetic differentiation observed likely reflects the separation of river systems by extensive landmass and mountainous terrain, which restricts the connectivity of aquatic habitats. Conservation and management strategies for these populations should consider these genetic distinctions, focusing on preserving both subpopulations and identifying potential aquatic corridors, such as coastal routes, to facilitate connectivity and maintain genetic diversity.

The AMOVA results, combined with the pairwise F_{ST} estimates, provide further understanding of the genetic differentiation between and within the East and West Coast groups. The AMOVA analysis shows that a substantial 71.40% of the total genetic variation is attributed to differences among the East and West Coast groups, as indicated by the high variance component ($Va = 4.91167$) and a significant p-value ($p = 0.02835$). This suggests that the East and West Coast populations represent distinct genetic units. Similar findings have been observed in *C. niloticus* populations in Africa, where significant differentiation between Eastern Africa and Western Africa was attributed to large-scale geographic barriers limiting gene flow (Hekkala *et al*., 2010). The marked genetic divergence between the East and West Coasts supports the hypothesis of restricted connectivity, possibly reinforced by the unique hydrological and ecological characteristics of the two regions.

The pairwise F_{ST} values further emphasize the genetic differentiation identified in the AMOVA results. For example, the F_{ST} value of 0.75764 between the East and West Coast groups confirms their genetic separation. Within the West coast, populations such as Klias and Padas exhibit lower F_{ST} values (e.g., $F_{ST} = 0.03604$), indicating closer genetic connectivity. Conversely, the East Coast rivers exhibit higher pairwise F_{ST} values, such as between Kinabatangan and Silabukan ($F_{ST} = 0.84715$), reflecting higher genetic differentiation. The highest F_{ST} value (1.00000) between Kalumpang (East Coast) and Padas (West Coast) indicates complete genetic separation between both populations. These patterns align with findings in *C. acutus* populations, where river-specific isolation and limited gene flow resulted in distinct genetic clusters (Ross, 1998; Rossi *et al.*, 2021).

The AMOVA results also reveal that 19.53% of the genetic variation is explained by differences among populations within the same group ($Vb = 1.34374$, $p < 0.001$). Pairwise F_{ST} values within the East coast group indicate moderate connectivity in some cases, such as between Paitan and Serudong ($F_{ST} = 0.21959$), while others, such as between Segama and Silabukan ($F_{ST} = 0.53935$), suggest stronger genetic structuring. Such within-group differentiation could be driven by localized ecological factors or historical isolation events. Comparatively, studies on crocodilian populations in Southern Africa noted similar within-region genetic structuring due to ecological and hydrological barriers, further supporting these observations (Versfeld, 2016).

Finally, only 9.01% of the genetic variation was attributed to within-population diversity ($Vc = 0.62367$, $p < 0.001$), which is consistent with the low haplotype diversity observed within most rivers. This highlights the strong influence of localized genetic drift and founder effects, especially in isolated or small populations (Allendorf *et al.,* 2012). Together, the AMOVA and F_{ST} results underline the strong population structuring in *C. porosus* in Sabah, revealing the substantial influence of both large-scale geographic barriers and local ecological factors in shaping genetic diversity across the region.

Such hierarchical patterns of genetic differentiation are also well-supported by studies on other crocodilians. For example, Hekkala *et al*. (2010) noted that genetic differentiation between *C. niloticus* populations was driven by large-scale barriers, while within-region variation was lower due to localized gene flow and the relative genetic homogeneity of individuals within populations. Similarly, studies on *C. acutus* have demonstrated that within-population genetic diversity is typically constrained by founder effects, small population sizes, or limited genetic exchange, further reinforcing these observations (Rossi *et al*., 2021). Together, these findings emphasize that while localized gene flow can contribute to within-group or within-population diversity, the strongest genetic differentiation is often observed at broader geographic scales where connectivity is naturally more restricted. This highlights the importance of maintaining regional connectivity to support genetic diversity in fragmented populations.

In contrast to the strong genetic differentiation observed between the East and West Coast populations of *C. porosus*, studies on other species in Sabah have revealed different patterns of genetic structure. For example, research on the proboscis monkey found minimal genetic differentiation between populations in the Klias Peninsula (West Coast) and two Eastern populations, despite the Crocker Range separating these regions (Munshi-South & Bernard, 2011). Proboscis monkeys are known to use riverine forests as dispersal corridors, with their swimming ability facilitating movement across waterways (Boonratana, 2000). While there are no contemporary records of proboscis monkeys crossing the Crocker Range, the sharing of haplotypes between eastern and western populations may represent historical connectivity, possibly dating back to recolonization events from Crocker Range refugia after the last glacial maximum (Tanaka *et al*., 2001). Alternatively, a continuous historical distribution along the West Coast could have allowed for gene flow through isolation by distance. Unlike proboscis monkeys, *C. porosus* is restricted to aquatic habitats and does not traverse significant landmass or mountainous regions, which likely explains the pronounced genetic differentiation observed between their East and West Coast populations.

The mismatch distribution for the state-wide population and the East and West Coast populations shows contrasting patterns. The whole population exhibits a bimodal distribution with two prominent peaks, which also closely resembles the mismatch distribution of the East Coast population. This suggests that the genetic structure of the whole population may be heavily influenced by the East Coast population. In contrast, the West Coast population shows a unimodal distribution.

Understanding the mismatch distribution patterns provides crucial insights into the demographic history of populations. A unimodal distribution, characterized by a single peak in the mismatch graph, indicates that most genetic differences within a population are concentrated around one value. This pattern is typically associated with a recent population expansion, where a population undergoes rapid growth following a bottleneck or founder event (Rogers & Harpending, 1992). During such expansions, genetic diversity remains relatively low because the population originates from a small number of founding individuals, and there has been limited time for mutations to accumulate. Over time, as the population grows, mutations spread throughout the population, but the genetic signature of the rapid growth results in a unimodal distribution.

In contrast, a bimodal distribution, showing two distinct peaks, suggests a more complex demographic history, such as the existence of genetically distinct subpopulations or multiple demographic events. This pattern may occur when a population comprises clusters of individuals with differing genetic histories, such as groups that were historically isolated but later merged or partially connected. For example, populations experiencing intermittent connectivity or historical admixture can show bimodal or multimodal patterns, reflecting the combination of distinct genetic pools (Excoffier, 2004). These patterns help researchers differentiate between populations that have undergone single events and those shaped by more dynamic processes.

A population expansion occurs when a population's size increases rapidly following an event such as colonization, habitat expansion, or recovery after a bottleneck (Wereszczuk *et al.*, 2017; Tchabovsky *et al.*, 2024). In such cases, most individuals in the population share a relatively recent common ancestry, leading to low genetic differentiation and a unimodal mismatch distribution. For example, Grigg & Kirshner (2015) reported that crocodilian populations recovering from severe declines often exhibit genetic patterns indicative of recent expansions.

Similarly, studies on aquatic organisms, such as marine turtles, have shown unimodal mismatch distributions linked to post-glacial recolonization events (Bowen *et al.*, 1998).

The bimodal structure observed in the East Coast population could therefore be a result of a complex demographic history. On the other hand, the West Coast population's single peak implies a more homogenous and simplified demographic history, likely reflecting reduced gene flow and more localized demographic stability. These patterns align with the notion of stronger population structuring between the East and West Coasts, as suggested by earlier AMOVA results and high pairwise F_{ST} values.

Upon observing the bimodal distribution of the East Coast population in the mismatch distribution analysis, further investigation was conducted to understand the factors driving this complex demographic pattern. Notably, the Paitan population displayed a bimodal distribution, while the other rivers in the East Coast population exhibited unimodal distributions. This raised the possibility that the Paitan population was influencing the overall mismatch distribution pattern of the East Coast population. To test this hypothesis, the Paitan population was excluded from the East Coast dataset, and the mismatch distribution was recalculated. Interestingly, without the inclusion of the Paitan population, the East Coast population exhibited a unimodal distribution, aligning with the patterns seen in the other rivers. This result strongly suggests that the unique genetic signature of the Paitan population, characterized by its bimodal distribution, is a genetically distinct sub-population. The distinctiveness of the Paitan population raises the intriguing possibility that it may harbour crocodiles originating from outside Sabah, potentially representing individuals with genetic lineages that differ from those commonly observed in other Sabah crocodile populations. This could indicate occasional immigration events or historical connections with other populations, further contributing to its unique genetic structure.

Similar to this, the state-wide population Bayesian Skyline plot appears to be heavily influenced by the demographic patterns of the East Coast population, as both show a sharp decline in effective population size and a subsequent plateau over millions of years. In contrast, the West Coast population exhibits a markedly different demographic history. Its flat and constant effective population size suggests a stable population size history, likely due to a smaller population size, or lower genetic diversity. The shorter evolutionary time span further supports the idea that the West Coast population may have a simpler demographic history, potentially resulting from more recent colonization or restricted gene flow. This disparity highlights the influence of geographic and historical factors on population dynamics within Sabah, with the East Coast (Paitan River in particular) acting as a reservoir of genetic diversity and historical stability, while the West Coast appears more genetically isolated and demographically distinct.

Bayesian Skyline Plots have been widely used to infer the demographic histories of various species (Drummond *et al*., 2005). While direct applications of BSPs to crocodilian populations are scarce, the methodology has been extensively employed in other taxa to reconstruct past population dynamics. For example, a study on two Mediterranean snake species (*Malpolon monspessulanus* and *Hemorrhois hippocrepis*) demonstrated demographic expansions during the Late Pleistocene, driven by favourable climatic conditions and habitat availability. These expansions were linked to glacial periods, when Mediterranean habitats expanded, and mountain regions served as refugia during harsher climates (Machado *et al*., 2021). In another study of the blue-spotted salamander (*Ambystoma laterale*), a population increase was identified preceding the Last Glacial Maximum within ice-free areas of North America. Following this, the species gradually expanded its range, culminating in its current distribution. This study highlights the salamander’s remarkable post-glacial transformation, establishing its present range after significant demographic and distributional changes (Perktas *et al*., 2023).

These studies demonstrate the value of BSPs in understanding population expansions and contractions during key historical periods, expanding our knowledge of species' evolutionary responses to historical pressures. BSPs are particularly useful for linking genetic data with ecological and climatic changes, enabling researchers to identify key periods of population growth or decline and correlate them with environmental events (Drummond *et al.,* 2005; Brito *et al*., 2014). By integrating genetic and ecological data, these methods provide valuable insights for conservation planning, allowing for a deeper understanding of population dynamics and the factors influencing genetic diversity across time (Hay *et al.,* 2010; Dutton *et al*., 2014).

The phylogenetic tree illustrates clear genetic structuring within the *C. porosus* population, which aligns with the haplotype network analysis. Notably, Haplotypes 5, 6, and 7, associated with the West Coast populations (Klias and Padas), form a distinct clade, demonstrating their genetic isolation from the East Coast populations. This West Coast clade supports the findings from the haplotype network, where these haplotypes were grouped together and confined to the West Coast. On the East Coast, Haplotypes 9, 11, and 12, exclusive to the Paitan population, form another unique clade. These haplotypes are genetically distant from the next closest haplotype within the East Coast population (Hap 8), separated by approximately 15 mutations. This distance is significant, highlighting the unique evolutionary history of the Paitan population within the East Coast group. Interestingly, the East and West Coast groups themselves are separated by approximately 12 mutations, suggesting that the genetic divergence between these two regional groups is slightly less pronounced than the internal divergence seen within the East Coast population between the Paitan haplotypes and the rest of the East Coast haplotypes. Additionally, within the East Coast group, there is further structuring, for instance, Haplotypes 8 and 10 cluster closely together, forming a sub-group within the East Coast populations. Similarly, Haplotypes 17 and 19 (associated with Serudong and Segama) form another East Coast clade. These sub-groupings reflect localized genetic differentiation likely driven by limited gene flow and historical isolation among East Coast rivers.

The placement of *C. siamensis* as the basal outgroup in the phylogenetic tree of *Crocodylus* is supported by molecular studies and reflects its early divergence from other Indo-Pacific crocodile species. Research using mitochondrial DNA markers consistently identifies *C. siamensis* as diverging earlier than *C. porosus* and related taxa. Meganathan *et al.* (2010) conducted a comprehensive study using mitochondrial genomes, which provided robust support for the early divergence of *C. siamensis* within the genus. This divergence likely occurred during the late Miocene to early Pliocene, approximately 5 to 10 million years ago, as estimated by molecular clock analyses. Fossil evidence also supports this timeline, indicating that *C. siamensis* represents an early branching lineage within the *Crocodylus* clade.

Ecologically, *C. siamensis* is primarily found in freshwater habitats across mainland Southeast Asia, distinct from the predominantly coastal and estuarine habitats of *C. porosus*. This geographic and ecological isolation has likely contributed to the genetic and evolutionary distinctions between the species. Studies by Meredith *et al*. (2011) and Oaks (2011) have reinforced this basal position in phylogenetic analyses of crocodilians, providing a solid framework for understanding their evolutionary history.

The observed differentiation of Australian *C. porosus* haplotypes from Sabah haplotypes highlights regional genetic structuring within this widely distributed species. *C. porosus* spans a vast range from Southeast Asia to northern Australia, and genetic studies have identified mitochondrial DNA divergence between populations in these regions. For example, FitzSimmons *et al.* (2002) and Sajeev *et al*. (2019) documented distinct haplotypes in Australian populations compared to those in Sabah. Interestingly, while the Australian sample exhibits a long branch length, indicating substantial divergence, it clusters with the Eastern Sabah samples in the phylogenetic tree. This suggests a closer relationship to the more diverse Eastern Sabah population, which could reflect historical connectivity or shared ancestry. The genetic differentiation observed is likely a result of limited gene flow across geographic distances, compounded by local adaptation and historical population dynamics. During the Pleistocene glacial cycles, sea-level fluctuations and habitat fragmentation may have isolated populations in different refugia, fostering genetic divergence, while occasional connectivity may have facilitated some shared genetic traits. The genetic structuring observed within *C. porosus* populations has important implications for conservation and management. Therefore, preserving these regional populations is essential for maintaining the overall genetic diversity of the species, which can enhance its resilience to environmental changes.

To backtrack and revisit an earlier analysis, it is important to highlight findings from the genetic variation analysis conducted specifically for the D-loop marker. Unlike the concatenated dataset used for the primary analyses, the D-loop marker analysis included four additional samples from problematic adult crocodiles captured in urban areas of Kota Kinabalu. These unique samples provided valuable insights into potential movement patterns. One of these samples, TRS, from Tuaran, shared the same haplotype (Hap 11) as individuals from the Paitan population in the northeast of Sabah. Since this haplotype is unique to Paitan River and was not found in other populations, there is a very high possibility that this individual travelled via coastal routes from

Paitan to the city centre on the West Coast, demonstrating the possible connectivity between distant populations through historical or occasional coastal migration.

Similarly, another sample, PGS, from Pulau Gaya, an island off the coast of Kota Kinabalu, shared the same haplotype (Hap 7) as individuals from the Klias River population. Given the close geographical proximity of Pulau Gaya to the Klias River (as shown in Figure 5.1), it is plausible that this individual travelled from the Klias River into the sea and eventually to the island. These findings, derived from the D-loop marker, underscore the importance of revisiting individual marker analyses, particularly when additional samples offer insights into localized or unique dispersal events. By incorporating these observations, we gain a deeper understanding of the movement and connectivity patterns of *C. porosus*, especially in areas where such patterns might not be apparent in the concatenated dataset.

These findings provide compelling evidence that *C. porosus* individuals in Sabah are still utilizing coastal routes for movement and dispersal, even in the face of anthropogenic pressures and disturbances. Despite the potential barriers posed by urbanization, habitat modification, and increased human activity, the identification of haplotypes shared between geographically distant populations suggests that the sea continues to play a crucial role in maintaining connectivity among crocodile populations. This also reaffirms the ability of *C. porosus* in exploiting marine environments as dispersal corridors.

Such dispersals are vital for maintaining genetic diversity within *C. porosus* populations. The mixing of individuals from different populations reduces the risks associated with inbreeding and genetic drift, which can threaten isolated populations. Coastal dispersal allows for gene flow across river systems, ensuring the exchange of genetic material that supports the long-term viability and adaptability of the species. This demonstrates the importance of preserving not only riverine habitats but also the coastal environments that facilitate these connections. Effective conservation strategies should account for the ecological significance of coastal dispersal and aim to mitigate the impact of human activities on these crucial migration pathways.

CHAPTER 5

Population Viability Analysis (PVA) of the Estuarine Crocodile Population in Sabah and its Implication for Management: An Overall Summary

5.1 Introduction

Population Viability Analysis (PVA) is a process and a powerful tool used in conservation biology that involves evaluating data and models to assess the probability of a population's persistence over a specified period in the future. PVAs use mathematical models to simulate population dynamics, allowing researchers to estimate the probability of a population's extinction or persistence under different scenarios (Morris & Doak, 2002). By incorporating factors such as survival rates, reproduction, environmental variability, and carrying capacity, PVA provides insight into how a species' population might respond to various threats, such as habitat destruction, climate change, or overharvesting.

At its core, PVA involves projecting future population trends by applying specific demographic parameters to generate forecasts of population sizes over time. It typically combines stochastic models (which incorporate randomness) and deterministic models (which assume fixed parameters) to predict the range of possible outcomes. These models can be particularly useful for assessing small or fragmented populations, where the risk of extinction is higher due to factors like inbreeding, reduced genetic diversity, or small effective population size (Shaffer, 1981; Lande, 1993).

PVA is used to inform conservation management strategies, as it helps prioritize efforts by identifying populations that are at the highest risk of extinction and suggesting appropriate interventions (Bruford *et al.*, 2010; Gardner *et al.*, 2021). For example, PVAs can be used to determine whether a population's current size is sufficient to ensure its survival over a given timeframe, or to test the effectiveness of different conservation actions, such as habitat restoration or translocation programs (Bruford *et al.*, 2010; Gardner *et al.*, 2021). In addition, PVA can provide a basis for setting conservation targets, such as the minimum viable population size (MVP) necessary to maintain a population's long-term viability (Frankham, 2005).

While PVA is a valuable tool, it is important to note that its predictions are dependent on the accuracy of the data and assumptions used in the model. Since PVA requires a detailed understanding of a species' ecology and demographic patterns, the results are often most reliable when based on long-term data from field studies, such as those on survival rates, reproductive success, and environmental factors that influence population dynamics (Kramer-Schadt *et al.*, 2009).

The C. *porosus* population in Sabah represents one of the most significant populations in Malaysia, with individuals found across the state's rivers. Through extensive field surveys and demographic analysis, it has been established that the *C. porosus* populations in these rivers today are generally stable, though fragmented, with varying densities across different rivers (present study). The population structure is marked by a mix of age classes, with hatchlings and yearlings being predominant, which suggests a relatively healthy breeding structure. However, these populations are not immune to threats such as habitat loss, human disturbance, and climate change, which continue to affect their long-term viability.

As mentioned earlier in this thesis, *C. porosus* is classified as "Least Concern" by the International Union for Conservation of Nature (IUCN) globally, yet the species faces significant local threats, particularly in Sabah. The primary threats are linked to human activities, including encroachment into their natural habitats, illegal hunting, and, more recently, human-crocodile conflicts. While crocodiles are protected under Malaysian wildlife laws, local populations often face challenges due to inadequate enforcement. Consequently, despite their relatively stable population in the wild, the crocodile population in Sabah requires continuous monitoring and conservation actions to mitigate human-induced pressures.

In recent years, human-crocodile conflicts have escalated as a major conservation issue in Sabah, particularly in areas where human settlements and agricultural activities overlap with crocodile habitats. This conflict is most severe along the Kinabatangan River, where populations of *C. porosus* are dense, and riverine development projects have reduced the natural buffer between crocodiles and human settlements. The growing frequency of such conflicts has led to public outcry and calls for more proactive management measures, including the culling of problematic crocodiles.

To address these concerns, the Malaysian government has voiced its intention to implement a harvest program that targets the removal of "problematic" crocodiles from rivers and other inhabited areas (Sabah Wildlife Department). The goal of this program is to reduce the risk of human-crocodile conflicts by removing crocodiles that pose a threat to public safety. However, the effectiveness of such a program depends heavily on understanding the local population structure, movement patterns, and long-term viability, which is where PVA becomes an invaluable tool.

This PVA will provide essential insights into the potential impacts of a proposed harvest program on the long-term sustainability of the *C. porosus* population in Sabah. By simulating different scenarios that include both natural population dynamics and the removal of individuals, the PVA can predict the consequences of harvesting on the overall population size. Through demographic modelling, the PVA offers a clearer understanding of how selective removal of crocodiles, especially large or "problematic" individuals, may affect the reproductive success, and long-term viability of the population. Additionally, the model can test the potential risks of overharvesting and the possible need for alternative management strategies, such as relocation to protect both human populations and crocodiles.

By providing data-driven predictions, the PVA can guide decision-makers in crafting a harvest program that balances public safety with the need to conserve the species. Moreover, this analysis highlights the importance of considering not only immediate population impacts but also the potential long-term ecological consequences of harvesting. Given that *C. porosus* is a keystone species in its ecosystem, any disruption in its population dynamics could have cascading effects on the broader ecosystem. Therefore, the PVA results will play a crucial role in informing both policy and management strategies aimed at reducing conflict while ensuring the species' persistence in Sabah.

Primary objective

To determine extinction rates for natural populations of *C. porosus*, as well as for populations under a managed harvest plan.

5.2 Methodology

The Population Viability Analysis (PVA) for *C. porosus* in Sabah was conducted using Vortex version 10 (Lacy, 2009), a widely used software tool designed for modelling population dynamics and assessing extinction risks based on demographic, genetic, and environmental factors. The parameters applied in the PVA are shown in Table 5.1.

Table 5.1. Vortex parameters used for the baseline model of *C. porosus.*
See text for more details.

<table>
<tr><th rowspan="3"></th><th rowspan="3">RIVER</th><th colspan="3">REPRODUCTIVE RATES</th><th>MATE MONOPOLIZATION</th><th rowspan="3">INITIAL POPULATION SIZE</th><th rowspan="3">DENSITY/ KM</th><th rowspan="3">CARRYING CAPACITY</th></tr>
<tr><th rowspan="2">% adults breeding</th><th colspan="2">Distribution of broods per year</th><th rowspan="2">% of males in breeding pool</th></tr>
<tr><th>0</th><th>1</th></tr>
<tr><td rowspan="10">1</td><td>Klias</td><td>100</td><td>70</td><td>30</td><td>50</td><td>41</td><td>0.95</td><td>76</td></tr>
<tr><td>Padas</td><td>100</td><td>60</td><td>40</td><td>50</td><td>12</td><td>0.29</td><td>35</td></tr>
<tr><td>Kinabatangan</td><td>100</td><td>50</td><td>50</td><td>50</td><td>336</td><td>2.10</td><td>1176</td></tr>
<tr><td>Segama</td><td>100</td><td>70</td><td>30</td><td>50</td><td>74</td><td>2.46</td><td>369</td></tr>
<tr><td>Silabukan</td><td>100</td><td>50</td><td>50</td><td>50</td><td>28</td><td>0.46</td><td>60</td></tr>
<tr><td>Bengkoka</td><td>100</td><td>75</td><td>25</td><td>50</td><td>23</td><td>0.41</td><td>25</td></tr>
<tr><td>Paitan</td><td>100</td><td>50</td><td>50</td><td>50</td><td>33</td><td>0.83</td><td>50</td></tr>
<tr><td>Kalumpang</td><td>100</td><td>60</td><td>40</td><td>50</td><td>71</td><td>1.47</td><td>118</td></tr>
<tr><td>Labuk</td><td>100</td><td>75</td><td>25</td><td>50</td><td>13</td><td>0.17</td><td>20</td></tr>
<tr><td>Serudong</td><td>100</td><td>60</td><td>40</td><td>50</td><td>30</td><td>0.56</td><td>56</td></tr>
<tr><td rowspan="9">2</td><th colspan="8">REPRODUCTIVE SYSTEM</th></tr>
<tr><td colspan="5">Age of 1st offspring (female)</td><td colspan="3">10</td></tr>
<tr><td colspan="5">Age of 1st offspring (male)</td><td colspan="3">16</td></tr>
<tr><td colspan="5">Max. age of reproduction (female)</td><td colspan="3">50</td></tr>
<tr><td colspan="5">Max. age of reproduction (male)</td><td colspan="3">60</td></tr>
<tr><td colspan="5">Max. lifespan</td><td colspan="3">90</td></tr>
<tr><td colspan="5">Max. no. of progeny per brood</td><td colspan="3">60</td></tr>
<tr><td colspan="5">Max. no. of brood per year</td><td colspan="3">1</td></tr>
<tr><td colspan="5">Birth sex ratios</td><td colspan="3">50:50</td></tr>
<tr><td rowspan="7">3</td><th colspan="5">MORTALITY RATES</th><th colspan="2">VALUE</th><th>SD</th></tr>
<tr><td colspan="2" rowspan="3">Females</td><td colspan="3">0-1 years</td><td colspan="2">50</td><td>10</td></tr>
<tr><td colspan="3">1-2 years</td><td colspan="2">10</td><td>3</td></tr>
<tr><td colspan="3">>2 years</td><td colspan="2">1</td><td>0.3</td></tr>
<tr><td colspan="2" rowspan="3">Males</td><td colspan="3">0-1 years</td><td colspan="2">50</td><td>10</td></tr>
<tr><td colspan="3">1-2 years</td><td colspan="2">10</td><td>3</td></tr>
<tr><td colspan="3">>2 years</td><td colspan="2">1</td><td>0.3</td></tr>
</table>

5.2.1 PVA Setup and Parameters

The PVA for *C. porosus* in Sabah was based on demographic data from 10 rivers, with key parameters such as population size, carrying capacity, age structure, and sex ratio derived from field surveys. Population size was estimated through direct counts across river segments, with density estimates for juveniles, subadults, and adults used to model population structure. While these estimates provide a strong foundation, future refinements using capture-mark-recapture or genetic methods could improve accuracy. The sex ratio was assumed to be 50:50, reflecting natural expectations, though potential biases due to differential survival or dispersal should be considered. Reproductive parameters (age of first reproduction, maximum reproductive age, and clutch size) were based on published literature, with future field studies needed to refine these estimates for Sabah. Mortality rates followed previous studies, with adult survival at 70-90% and lower rates for juveniles, aligning with expected early-life mortality. However, incorporating long-term survival data could enhance model reliability. To account for environmental uncertainty, a 10% SD was applied to breeding success, capturing natural fluctuations. While this approach improves realism, empirical nesting data would further refine projections. These parameters represent the best available estimates, but future research such as long-term monitoring and ecological studies could improve model accuracy for conservation planning.

5.2.2 Simulation Parameters

The Vortex 10 simulation was run for 100 years with annual time steps to evaluate long-term population viability. A logistic growth function was employed, with a growth rate (r) of 0.03 and carrying capacity (K) determined by habitat and resource availability. Various scenarios were tested, including a baseline no-harvest scenario, and several harvest scenarios simulating the removal of problematic crocodiles to address human-crocodile conflict. The model incorporated density-dependent reproduction, where breeding success declined as population density increased, and considered the Allee effect, where reproduction could be impaired at very low population sizes. Stochastic simulations were used to account for demographic and environmental randomness, including variability in survival, reproduction, and environmental conditions. The initial age structure was derived from field data, and the sex ratio was set at 50% male and 50% female for all populations.

5.2.3 Running Simulations

After inputting the data and setting parameters, Vortex 10 was used to simulate the population dynamics of *C. porosus* over 1000 iterations. Each iteration represented a unique set of random events, reflecting the inherent uncertainty in survival and reproduction. The main outputs from the simulations included population size trajectories, extinction probability, and mean time to extinction. Additionally, the effects of different management strategies, including harvest programs and the introduction of supplementary individuals, were evaluated. The simulations assessed how removing problematic crocodiles influenced population stability and tested the potential for introducing individuals to bolster population size and mitigate decline. Results were analyzed to determine the effectiveness of population control measures and highlight the risks of overharvesting, underlining the need for sustainable management strategies to reduce extinction risk.

5.3 Results

The results of the first simulation reveal survival probabilities and population sizes across *C. porosus* populations in Sabah in 100 years, under natural conditions without harvest intervention (Figure 5.1). The Kinabatangan population (represented by the green line) and the metapopulation (represented by the purple line) exhibit a relatively steady survival trajectory compared to the other populations. The Kinabatangan population starts with a strong survival probability, gradually declining around year 70, with the metapopulation following a similar trajectory shortly after, beginning its decline around year 75. Initially, both populations maintain high survival rates, with the metapopulation staying close to a 1.0 survival rate for the first 60-70 years, influenced by the relatively stable Kinabatangan population. The Kinabatangan population's decline in survival probability mirrors that of the metapopulation, suggesting that the metapopulation is heavily influenced by the dynamics of the Kinabatangan River population. As the Kinabatangan population declines over time, the metapopulation also starts showing similar patterns of decline, indicating that the large and resilient Kinabatangan population plays a significant role in the long-term persistence of the crocodile population across the region.

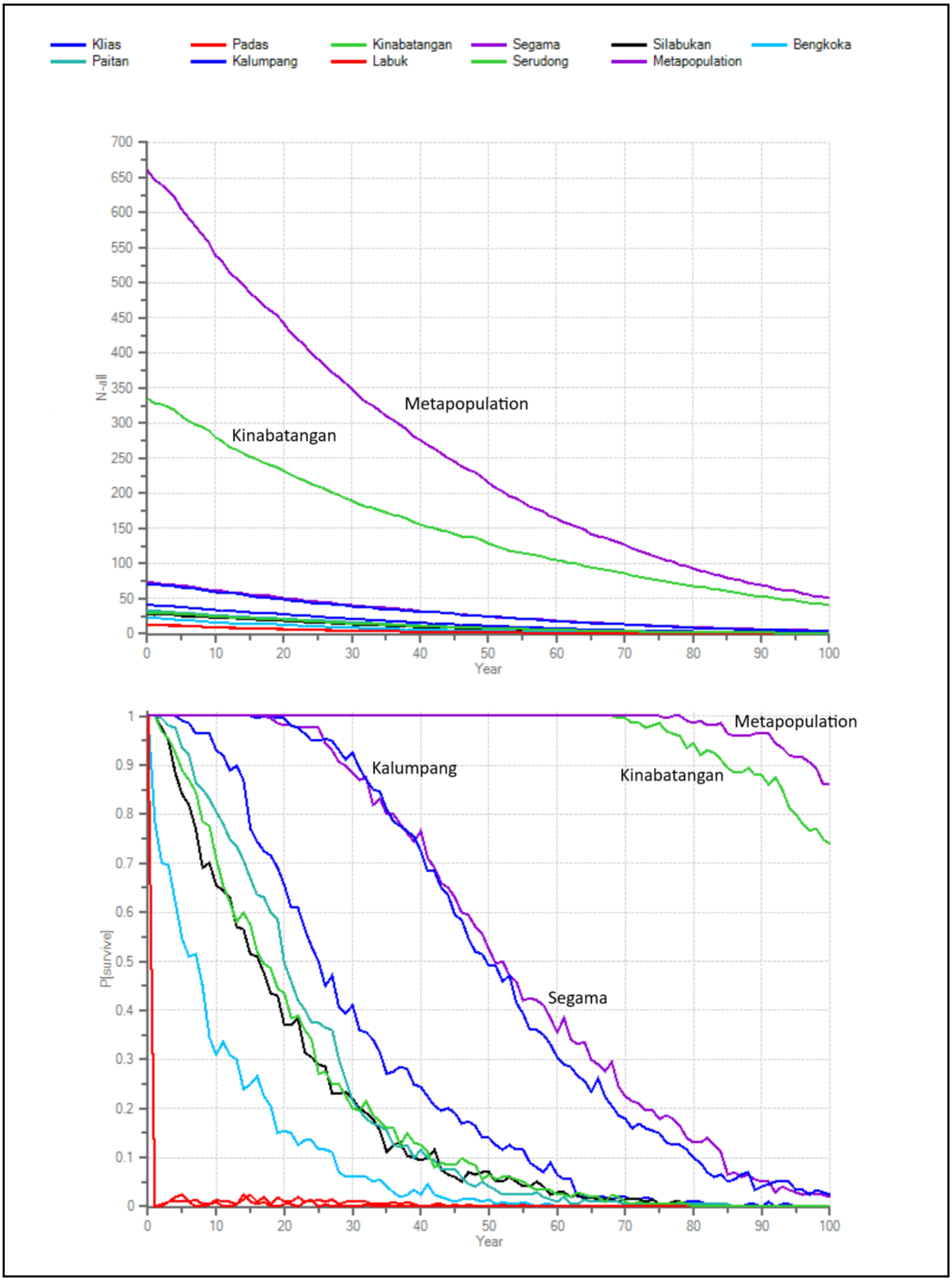


Figure 5.1 Survival probability and population size of *C. porosus* populations in Sabah in a natural setting.

In contrast, smaller populations, such as Labuk and Padas, exhibit immediate and sharp declines in their survival probabilities, approaching extinction within 30 years. These populations show rapid decreases in survival rates to nearly 0, with no clear stabilization over time. This suggests that smaller populations are more vulnerable to stochastic events, environmental variability, or demographic constraints, which cause them to decline much faster than the larger populations. Other populations, such as those in Kalumpang, Segama, Bengkoka, Silabukan, Serudong, Paitan, and Klias, experience steady declines in both survival probabilities and population size, although at varying rates. Kalumpang and Segama decline at a similar pace, maintaining very low survival rates (below 0.1) at the 100-year mark but manage to survive beyond year 100. On the other hand, Bengkoka reaches extinction around year 50, and populations in Silabukan, Serudong, Paitan, and Klias reach extinction in the 70–80-year timeframe.

Following this, an assessment of individual populations was done through simulations that included both a harvest intervention and the introduction of supplementary individuals. Harvest intervention was not simulated for Padas and Labuk Rivers due to their drastic population decline. Likewise, supplementary intervention was not simulated for Kinabatangan River due to their sustainable population under natural conditions. Figure 5.2 shows the simulations carried out for Padas and Labuk Rivers, the two rivers that indicate an extinction in less than 30 years.

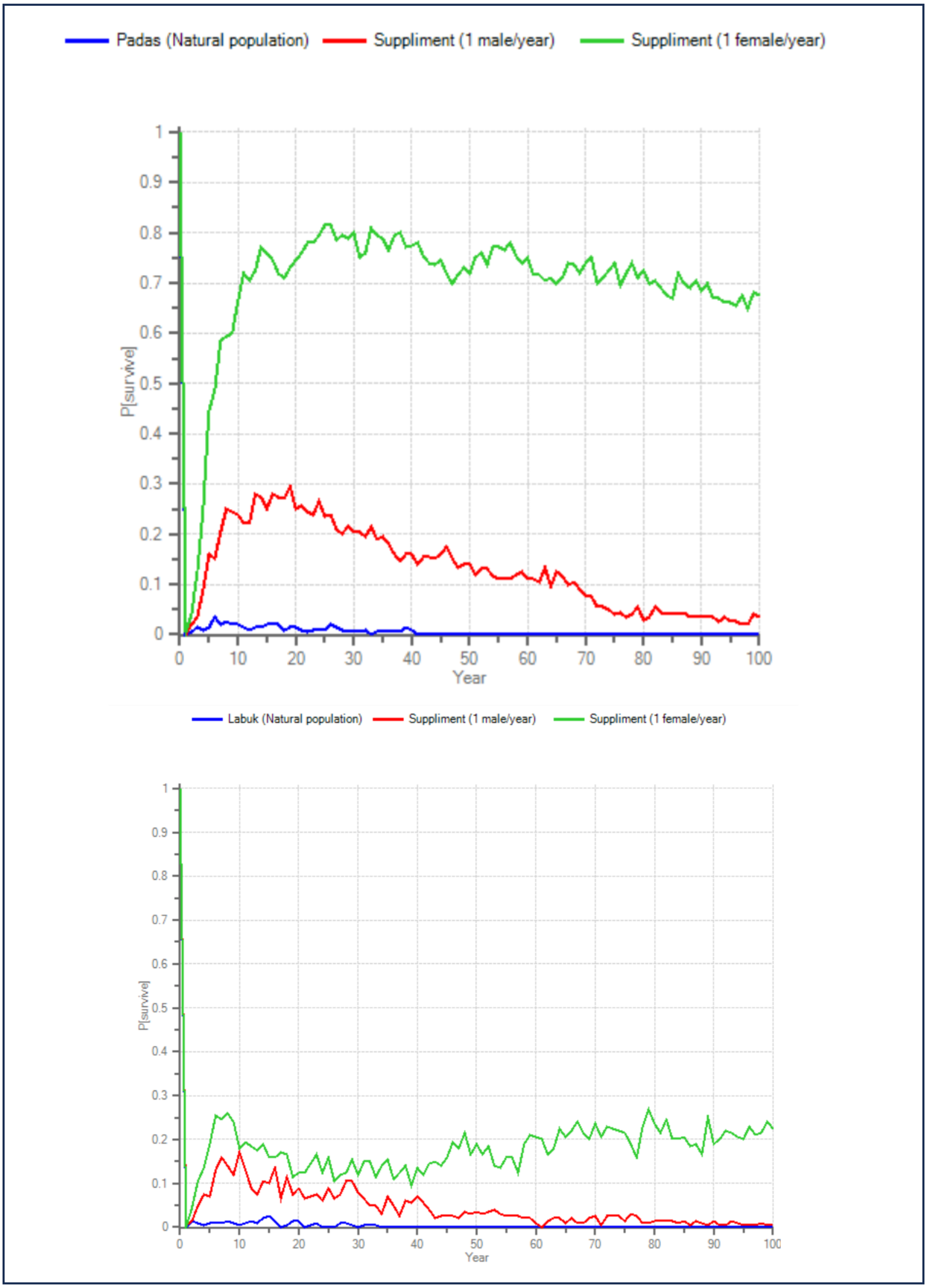


Figure 5.2 Survival probability of *C. porosus* populations in Padas River and Labuk River under natural settings (blue), with a supplement of 1 male/year (red), and a supplement of 1 female/year (green).

Both the Padas and Labuk populations exhibit a sharp decline in survival probabilities under natural conditions, with extinction occurring by year 30. However, the introduction of supplementary individuals improves survival rates in both populations. In both cases, adding 1 male per year results in an initial increase in survival probability, but the improvement is less sustained compared to the scenario with 1 female per year. The female supplementation scenario shows a more pronounced and lasting positive effect, with survival probabilities stabilizing at higher levels over the 100-year period.

The remaining rivers were simulated with an addition of a harvest intervention (Figures 5.3 - 5.9).

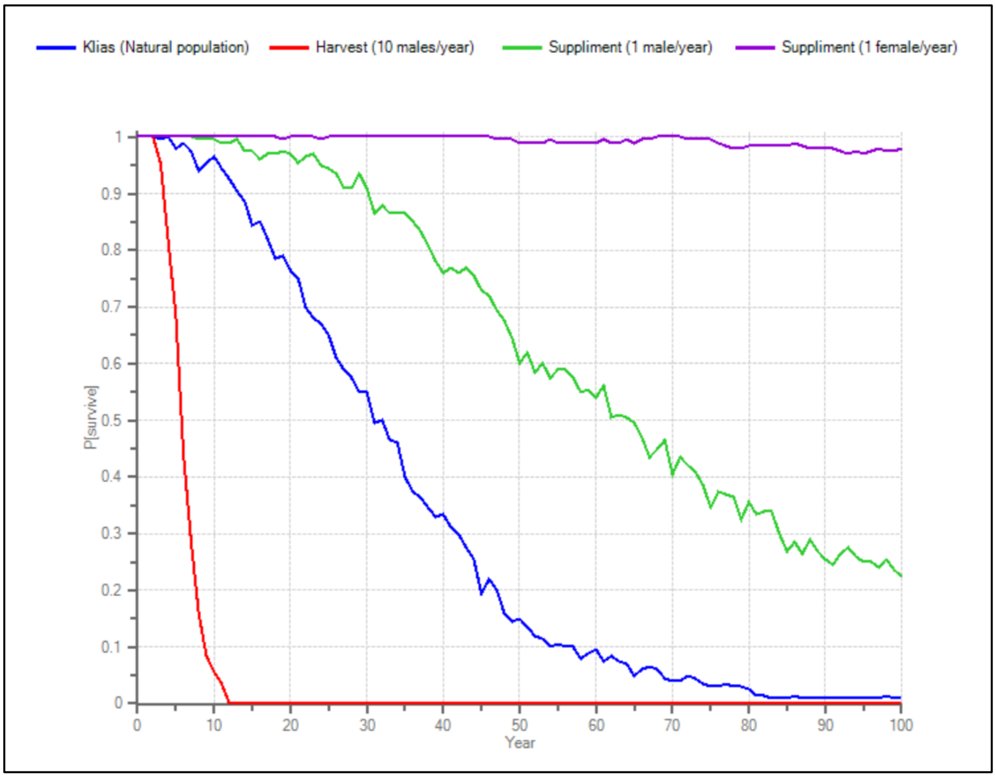


Figure 5.3 Survival probability of *C. porosus* population in Klias River under natural settings (blue), with a supplement of 1 male/year (green), a supplement of 1 female/year (purple), and a harvest of 10 males/year (red).

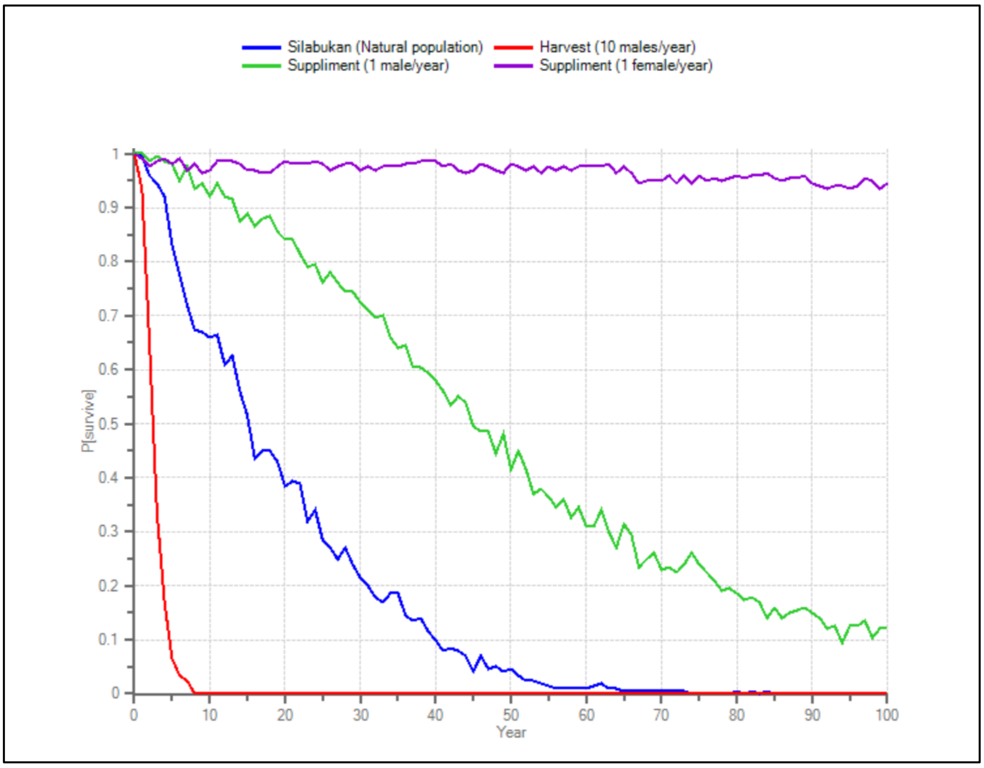


Figure 5.4 Survival probability of *C. porosus* population in Silabukan River under natural settings (blue), with a supplement of 1 male/year (green), a supplement of 1 female/year (purple), and a harvest of 10 males/year (red).

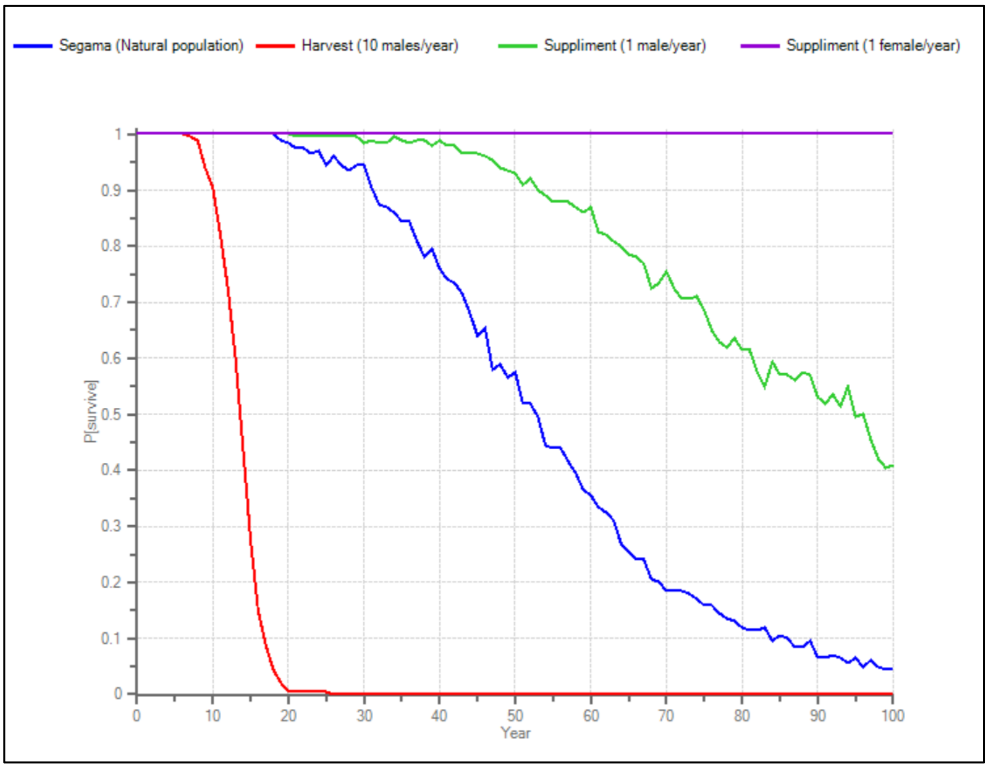


Figure 5.5 Survival probability, of *C. porosus* population in Segama River under natural settings (blue), with a supplement of 1 male/year (green), a supplement of 1 female/year (purple), and a harvest of 10 males/year (red).

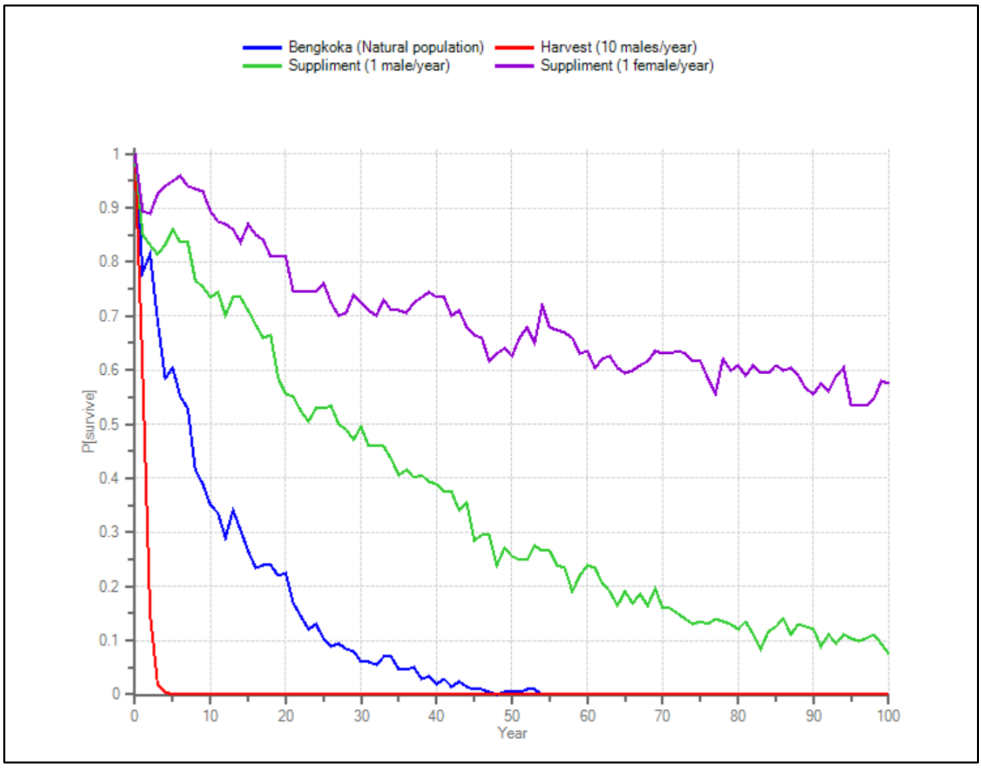


Figure 5.6 Survival probability of *C. porosus* population in Bengkoka River under natural settings (blue), with a supplement of 1 male/year (green), a supplement of 1 female/year (purple), and a harvest of 10 males/year (red).

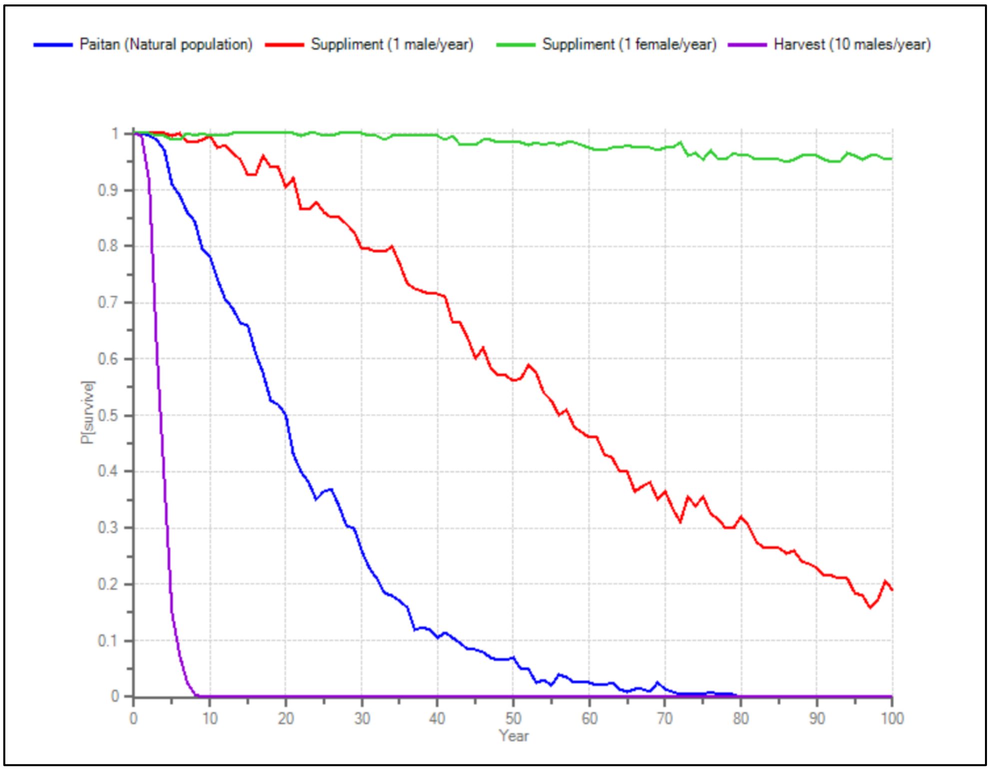


Figure 5.7 Survival probability of *C. porosus* population in Paitan River under natural settings (blue), with a supplement of 1 male/year (red), a supplement of 1 female/year (green), and a harvest of 10 males/year (purple).

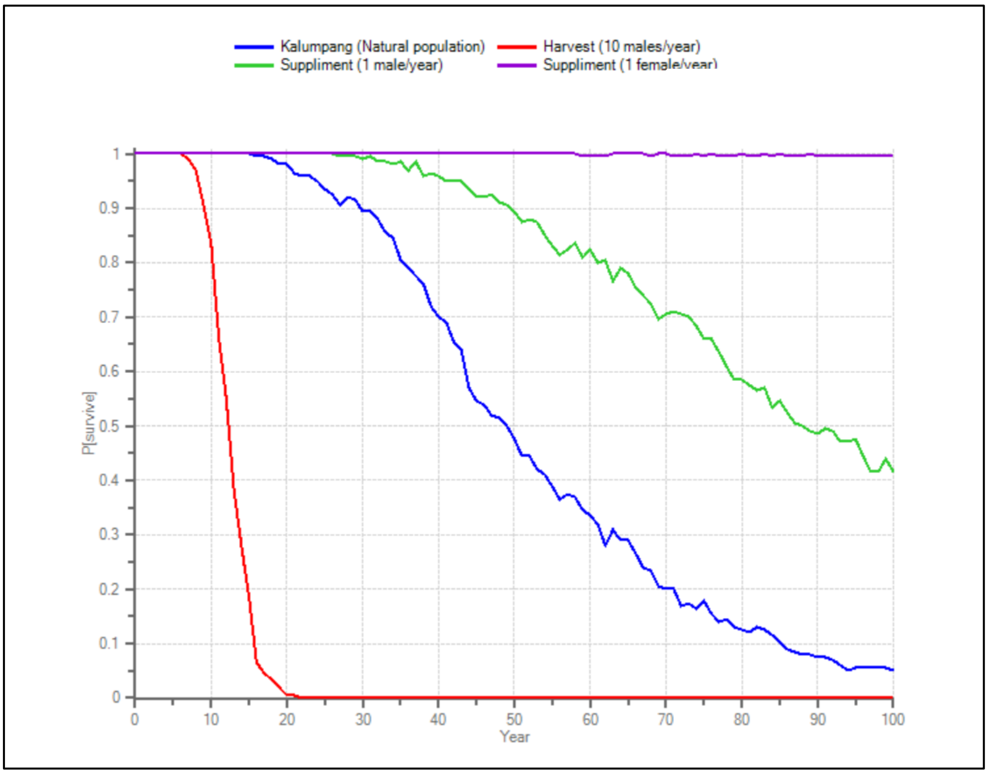


Figure 5.8 Survival probability of *C. porosus* population in Kalumpang River under natural settings (blue), with a supplement of 1 male/year (green), a supplement of 1 female/year (purple), and a harvest of 10 males/year (red).

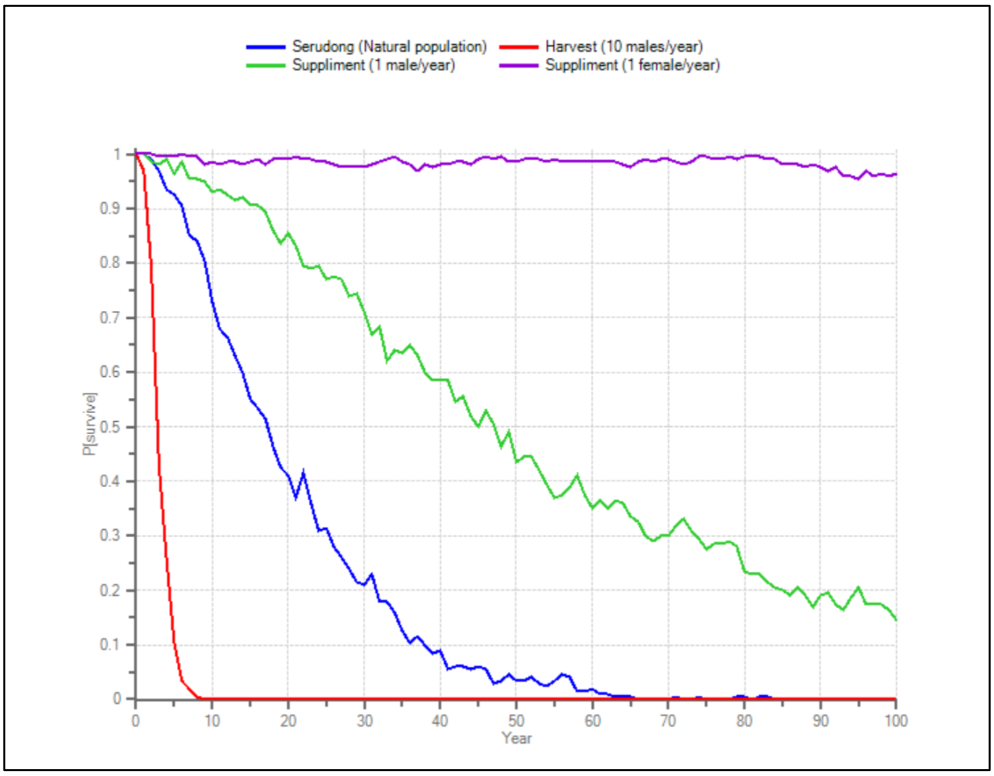


Figure 5.9 Survival probability of *C. porosus* population in Serudong River under natural settings (blue), with a supplement of 1 male/year (green), a supplement of 1 female/year (purple), and a harvest of 10 males/year (red).

The simulation results for the rivers above show that the *C. porosus* populations in Klias, Silabukan, Segama, Bengkoka, Paitan, Kalumpang and Serudong Rivers will experience extinction under a harvest scenario of 10 males/year. Bengkoka River shows the earliest extinction (year 5), while the other rivers show extinction between year 8 and 20. All these rivers, like Padas and Labuk Rivers, show improvements when a supplement is introduced to the population. A female supplement brings a higher survivability rate than a male supplement. The final river, Kinabatangan River was simulated with harvest interventions of 40 males/year, 20 males/year and 10 males/year as shown in Figure 5.10.

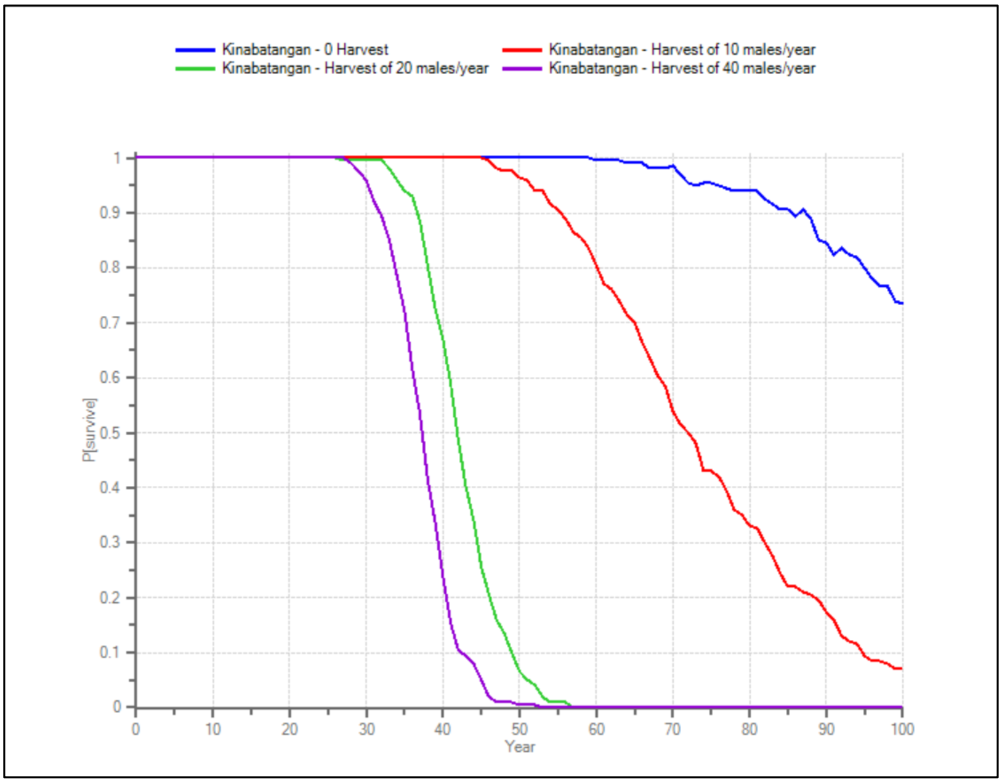


Figure 5.10 Survival probability of *C. porosus* population in Kinabatangan River under natural settings (blue), with a harvest of 40 males/year (purple), a harvest of 20 males/year (green), and a harvest of 10 males/year (red).

The harvest of 40 males per year leads to the sharpest decline in survival, with the population nearing extinction by year 50. This rapid decline highlights the significant pressure that such a high level of harvesting places on the population, drastically reducing its ability to persist in the long term. The harvest of 20 males per year shows a similarly negative impact, though the population survives slightly longer, with extinction occurring around year 60. In the case of a harvest of 10 males per year, the population does not reach extinction by year 100 but still faces a significant decline. The gradient also indicates a continuous drop in survival rates, potentially causing extinction by year 110-120.

5.4 General Discussion

The survival rates of the *C. porosus* populations across Sabah provide valuable insights into the long-term viability of these populations under various management interventions. The results indicate that all populations, under natural conditions, face declines in survival probabilities over a 100-year period, with many populations reaching extinction within 50 to 100 years. Furthermore, it is evident that harvesting accelerates the decline of these populations, emphasizing the need for cautious management strategies that balance harvest with conservation goals.

The patterns observed from the simulations highlight the critical role of the Kinabatangan population in the overall dynamics of the metapopulation. Although all populations (except Kinabatangan) show significant population declines within the first 15 years, the metapopulation remains stable for a longer period, suggesting that the Kinabatangan population has a disproportionate impact on maintaining the stability of the overall population across the region. The Kinabatangan population's relative stability in the initial years helps buffer the other populations, delaying the inevitable decline of the metapopulation. However, once the Kinabatangan population begins to decline around year 70, the metapopulation follows suit, indicating that the Kinabatangan population's persistence is crucial for the survival of the metapopulation in the long term.

Populations in smaller rivers such as Padas and Labuk, exhibit steep declines in survival probability, with extinction occurring as early as 20 years. Larger rivers demonstrate a slightly more stable trajectory, maintaining a higher survival rate for a longer period, although even these populations eventually face extinction within the 100-year simulation period.

The importance of large population sizes in enhancing population viability and ensuring long-term survival has been well-documented in conservation biology. Several studies highlight that larger populations are more resilient to the negative effects of demographic stochasticity and environmental variability. For instance, Lande (1993) emphasizes that populations with larger sizes have a better ability to maintain stable birth and death rates, which are crucial for persistence over time. Brook & Bradshaw (2006) further support this, showing that small populations are more vulnerable to extinction due to the amplified effects of random fluctuations, while larger populations exhibit greater stability and are less likely to experience drastic declines. Moreover, Morris & Doak (2002) argue that large populations are less susceptible to inbreeding depression and genetic drift, both of which can undermine the fitness of small populations, making them more prone to extinction.

In addition to demographic resilience, larger populations also benefit from greater genetic diversity, which enhances their ability to adapt to environmental changes and reduces their vulnerability to inbreeding and genetic drift. Larger populations provide a larger gene pool, which allows for greater evolutionary potential, making them more capable of responding to environmental stressors such as disease outbreaks, climate change, and habitat shifts (Morris & Doak, 2002).

The introduction/supplementation of individuals into a small population can significantly enhance its viability, particularly through the mechanisms of genetic diversity and demographic stability. Studies have shown that supplementation can counteract the effects of inbreeding depression, which is common in small populations, thereby improving reproductive success and overall population health. For example, the Florida panther (*Puma concolor coryi*) population, which was once critically small with only 20 to 30 individuals, suffered from inbreeding-related genetic defects such as undescended testicles and heart defects. In the mid-1990s, genetic analysis revealed that Texas pumas were genetically similar to the Florida population, leading to the introduction of Texas pumas to enhance genetic diversity (Kobilinsky, 2019.) This not only tripled the genetic variation within the population, but also resulted in an increase of individuals to 230.

An important observation in terms of supplementation across all populations is that the introduction of females appears to have a more substantial and lasting positive impact on survival rates compared to the introduction of males. This finding suggests that if interventions such as supplementation are implemented in the future, special consideration should be given to introducing female crocodiles for several reasons. First, females produce eggs and hatchlings, directly contributing to the increase in population size through reproduction, whereas males do not directly affect population growth in the same way (Briggs *et al.*, 2011).

Secondly, female crocodiles tend to be less aggressive and territorial than males, which reduces the likelihood of conflict within the introduced habitat. Males, being larger and more territorial, may cause disruption in the local population through aggression, particularly with other males. Furthermore, large males have been known to exhibit more aggression towards humans, posing potential risks in areas with human-crocodile interactions (Webb & Manolis, 1989). Therefore, focusing on female introductions could promote a more stable, sustainable approach to population recovery as they directly contribute to population growth through reproduction. Additionally, introducing females could minimize potential conflicts within the ecosystem and with human populations.

It is evident from the PVA that all *C. porosus* populations in this study show increased survival rates with the intervention of a supplementation. For Kinabatangan River alone, the scenario is slightly different. Given its greater resilience and persistence in the simulations, it may be the only river in Sabah that does not require supplementation. Instead, a controlled harvest plan could potentially be considered in this river to address human-crocodile conflict issues. Even in this case, any removal strategy must be executed with extreme care to ensure that it does not destabilize the population.

In the case of *C. porosus*, the removal or harvesting of individuals is often linked to human-crocodile conflict (HCC), and typically, larger (male) individuals are targeted. This selective removal, while potentially reducing immediate conflict risks, can have long-term negative effects on the population's viability. Studies on fishing and selective harvesting in other species highlight the impact of such practices. For instance, Law (2000) found that fishing is a highly selective process, targeting specific sizes and locations of populations, and sometimes favouring one sex over another, which can lead to skewed sex ratios and altered size distributions in the breeding population. Such practices may also result in a loss of genetic diversity, as only certain individuals are removed, leaving behind a less genetically diverse population.

Furthermore, consistent removal of larger individuals over time, as observed in some fish populations, leads to slow-growing and early-maturing individuals (Smith, 1999). This trend suggests that selective removal of large crocodiles could lead to a shift in the population dynamics of *C. porosus*. Over time, these changes could have profound effects on the reproductive success and survival of the population, as the reproductive dynamics would shift, potentially lowering the quality of offspring and overall population resilience.

Although these findings address other species, it still emphasizes the potential consequences of selective harvesting, especially in terms of how it can alter the genetic makeup and life-history traits of a population. The removal of large males could lead to a reduction in genetic diversity, and even though the Kinabatangan River shows resilience in the simulations, selective harvesting could still destabilize the population over time. Therefore, any potential harvest or removal strategy, even for Kinabatangan, must be carefully managed to avoid long-term genetic and demographic consequences. Based on the genetic diversity results, it would be prudent to prioritize populations with higher genetic diversity for harvest or removal, such as Paitan River and potentially, Silabukan River as these populations are better equipped to withstand the loss of individuals without compromising their long-term stability. Conversely, populations with limited genetic diversity, especially Padas River and Kalumpang River should be excluded from any harvest strategies to prevent exacerbating their vulnerability. It is crucial to integrate genetic monitoring into management decisions to ensure that interventions, including the removal of problem crocodiles, do not unintentionally disrupt key life-history traits or compromise population persistence.

The removal or harvest of individuals from the remaining populations in Sabah, particularly in smaller or more isolated river systems, must be approached with extreme caution. In small populations, the loss of even a few individuals can aggravate genetic drift, which leads to a further reduction in genetic diversity. Over time, the combined effects of demographic pressures and reduced genetic diversity can lead to the "extinction vortex," where populations become increasingly vulnerable to decline and are unable to recover despite ongoing conservation efforts.

In study conducted on the tapir populations in Brazil, the PVA indicated that Morro do Diabo State Park (MDSP) hosts a large, healthy and stable population of approximately 130 individuals. While this population is expected to persist over the next 100 years, its size is insufficient to sustain genetic diversity and is therefore not considered viable in the long term (Medici & Desbiez, 2012). To ensure the long-term viability of tapirs in MDSP, a minimum viable population of 200 individuals was required. Therefore, targeted conservation strategies that focus on increasing the carrying capacity of the park and preserving at least 95% of the species' genetic diversity was necessary. Similarly, the focus for small *C. porosus* populations in Sabah should be to increase the carrying capacity.

Studies have shown that harvesting, particularly in populations with already low genetic diversity, can result in genetic bottlenecks, reduced reproductive success, and impaired adaptability, ultimately compromising the long-term survival of the species (Allendorf & Ryman, 2002; Frankham, 2005). The risk of genetic depletion is further demonstrated by studies on overharvesting in other species, such as marine turtles and large predators, where the removal of individuals has led to significant genetic loss. This depletion has hindered these species' ability to adapt to environmental changes and reduced their overall resilience. In the case of *C. porosus* populations in Sabah, the low genetic diversity observed in rivers like Kalumpang and Padas makes these populations particularly susceptible to such genetic bottlenecks. Therefore, any removal or harvest strategies must be carefully considered, with a focus on avoiding actions that could further deplete the genetic pool and compromise the long-term viability of these populations.

An intriguing aspect of the analysis lies in the contrast between the Kinabatangan River and the Paitan River populations. Despite Kinabatangan being the largest and most resilient in the PVA simulations, exhibiting a higher probability of survival over the long term, it surprisingly has low genetic diversity. In stark contrast, Paitan, with its high genetic diversity, faces much lower survival rates in the same simulations. This paradox highlights the complex interplay between genetic diversity and demographic factors, suggesting that while genetic diversity is important, it does not always guarantee population resilience in the face of environmental and demographic challenges.

A study by Willi & Hoffmann (2009) provides further insight into this issue, as it demonstrates how demographic factors often outweigh genetic factors in determining population persistence. Their model integrated quantitative genetics and demographic factors to assess population persistence under environmental change. The stochastic simulations revealed that demographic factors—particularly the intrinsic rate of natural increase (r) and the stochasticity of r—are more critical to long-term survival than genetic variation alone. The study showed that populations can persist despite low genetic diversity if they meet certain demographic thresholds.

However, when stochasticity in environmental variability becomes too high, populations fail to persist, regardless of genetic diversity. This highlights the importance of demographic resilience, which is the ability to maintain population growth rates and survival across fluctuating environmental conditions. While genetic diversity is important, it is not the primary factor driving population persistence, particularly when demographic factors such as population size, reproductive rates, and environmental stochasticity have a stronger influence (Willi & Hoffmann, 2009).

In the case of Paitan River, although the population exhibits high genetic diversity, the demographic factors may be more critical to its decline. The population's small size, compounded by environmental variability, likely overwhelms the genetic diversity that could otherwise help support long-term viability. As Willi & Hoffmann (2009) suggest, a population of size 20, for example, might lack the evolutionary potential not because of insufficient genetic variation, but because it fails to meet the necessary reproductive thresholds and is unable to withstand the demographic stochasticity (i.e., random fluctuations in population size). Thus, in the case of *C. porosus* populations like those in Paitan River, even a genetically diverse population may still face the risk of extinction due to demographic instability or insufficient reproductive rates, reinforcing the importance of demographic factors in PVA.

This observation partly explains why genetic factors were not included in the PVA, despite having conducted genetic analysis in this study. While genetic diversity is undeniably important for long-term population health, the results of the PVA demonstrate that demographic factors, such as population size and reproductive rates, play a more immediate and influential role in determining population viability. Additionally, genetic factors were excluded as a parameter in the PVA due to the limitation of using only one genetic locus (mtDNA). Although mtDNA provides valuable insights into historical gene flow and population structure, the use of multiple genetic loci (e.g., microsatellites or SNPs) would be more effective in a comprehensive PVA to capture the full genetic diversity of populations (pers. comm.).

Incorporating genetic analysis into Population Viability Analysis (PVA) is essential for understanding the long-term survival prospects of species. However, studies have shown that relying on a single locus can lead to significant limitations, as it may not adequately capture the complexity of genetic variation that influences a population's adaptability and resilience.

Conversely, multi-locus strategies provide a more comprehensive understanding by accounting for the interactions among various loci, thereby improving predictions related to population dynamics and viability. Thus, integrating multi-locus genetic data into PVA is crucial for accurately forecasting species viability in the face of environmental challenges.

Genetic diversity and demographic factors are certainly related, but one does not directly alter the other. While genetic diversity is crucial for a population's long-term adaptability and resilience to environmental changes, it does not directly influence demographic parameters such as birth rates, survival rates, or population size. However, demographic influences, such as population size, reproductive rates, and environmental pressures, can significantly affect genetic diversity. For example, small population sizes and low reproductive rates often lead to inbreeding, which reduces genetic variation over time through genetic drift (Frankham, 1996). Additionally, when populations are under demographic stress, such as in situations of habitat loss or over-exploitation, the resulting reduction in population size can further exacerbate genetic erosion, leading to the loss of beneficial alleles and decreased adaptive capacity (Allendorf & Luikart, 2007). Therefore, while high genetic diversity does not necessarily guarantee a thriving population, the loss of genetic variation due to demographic decline can severely compromise a population's long-term viability.

In a study on the population viability of the little owl (*Athene noctua*) in Europe, the declining population sizes of the populations indicated a drop in the genetic diversity of the little owl populations. This study incorporated both demographic and genetic factors into the PVA. However, genetic diversities did not affect the viability of populations as much as demographic factors did. When managing populations of little Owl within Europe, population size was an important factor to preserve genetic diversity and evolutionary potential (Andersen *et al*., 2017).

Genetic diversity can only be replenished through two primary processes: the immigration of individuals from other populations, which can introduce new genetic material, or through mutation, which results in random changes to the genetic code over. However, the role of mutation in maintaining genetic diversity is limited, as mutations occur infrequently, with only rare instances of increased mutation rates due to environmental factors like pollution or radiation. Over evolutionary timescales, mutation is the primary mechanism by which genetic variation is generated. Without this process, there would be little to no genetic diversity within populations. If the *C. porosus* populations in Sabah do not persist long enough, the process of mutation alone will be insufficient to maintain genetic diversity and will eventually reduce their survival chances.

The immigration of individuals from other rivers or areas, along with the introduction or supplementation of individuals, offers a promising strategy to improve the survivability of *C. porosus* in Sabah. Facilitating natural migrations between river systems, particularly between genetically distinct populations, could significantly enhance the genetic diversity and long-term viability of the species. As discussed in Chapter 4 (Movement), large crocodiles, including those from the Paitan River and Klias River, continue to utilize coastal areas for movement and migration. This behaviour could be strategically harnessed to promote gene flow between populations, especially from areas with higher genetic diversity, such as Paitan, to those with lower genetic diversity, such as those on the West Coast, which are classified as a separate sub-population. By enabling such migrations, not only would the overall population size increase, but the genetic diversity of the receiving populations would also improve, bolstering their ability to adapt to future challenges and reducing the risks extinction. This natural movement could, therefore, be a vital component of a comprehensive management strategy aimed at ensuring the long-term survival of *C. porosus* in Sabah.

This PVA serves as an initial stage of investigation into the long-term viability of the *C. porosus* populations in Sabah. It focuses on basic demographic parameters, such as population size and survival rates, but does not account for additional factors that could significantly alter the outcomes, such as catastrophic events like flooding, which can drastically impact population dynamics. Furthermore, the data used in this PVA was accumulated over a relatively short period of three years, which may not capture the full variability and long-term trends of a species like *C. porosus*, known for its long lifespan. Additionally, larger sample sizes are crucial for reliable PVA results. Given that the sample areas in this study may not have covered the entire river systems of each population, the PVA results might be underestimated, and thus, the actual population dynamics may differ from the predictions made here.

In a study on the *C. acutus* population in Colombia, the stochastic demographic analysis revealed that if this population remains below 500 individuals, there is a high probability that it will reach a state of quasi-extinction over the next 30 years (Ortega-Leon *et al.*, 2020) Although this finding is alarming, the authors highlighted two key observations that may temper the results. First, the sampling area in the study covered only a portion of the rivers and probably did not represent the full extent of the population. Furthermore, 6–8 years of data are generally recommended to generate more robust estimates in population variability analysis.

Thus, without sufficient data, the variability in simulations may not accurately reflect the natural variation of the population, which could lead to unreliable conclusions about population viability (Akçakaya & Sjögren-Gulve, 2000; Reed *et al.*, 2002). Therefore, it is crucial to consider the potential for underestimating population size in Sabah and to gather more long-term data to improve the accuracy of population viability assessments for *C. porosus*.

Nevertheless, despite the limitations of this PVA, it still provides valuable insights into the relative viability of different *C. porosus* populations in Sabah. While the analysis may not account for all potential factors or cover the full extent of each river system, it offers a comparative view of which populations are more at risk of extinction than others. The results highlight specific populations that are more vulnerable to demographic decline, such as those in smaller river systems, and allow for the identification of populations that may require more urgent management interventions. In this sense, the PVA provides a useful starting point for understanding population trends and setting priorities for conservation efforts, even if further data and analysis are needed for a more comprehensive assessment.

The stability of the *C. porosus* metapopulation in Sabah relies on a few critical factors. First and foremost, the protection and preservation of Kinabatangan River is essential. Second, it is crucial to maintain and, where possible, enhance the functional connectivity of the other rivers. Third, efforts must be made to neutralize any threats to *C. porosus* in the smaller and fragmented populations.

Besides providing an analysis of the PVA results, this chapter also serves an important role as a summary chapter that synthesizes the findings of the entire thesis. The chapter not only explores the demographic aspects of *C. porosus* in Sabah, but it also integrates the conclusions drawn from previous chapters on the genetic diversity and movement patterns of the species, providing a comprehensive overview of the species' long-term sustainability.

Ensuring the survival of *C. porosus* in Sabah while mitigating human-crocodile conflict requires a multifaceted approach that addresses both the ecological needs of the crocodile populations and the safety concerns of local communities. One key aspect is the establishment of buffer zones around crocodile habitats. These zones limit human encroachment into critical crocodile territories, particularly in river systems with high crocodile densities, such as the Kinabatangan River. Buffer zones could act as a physical barrier, reducing the chances of human-crocodile interactions while allowing crocodiles to maintain their natural behaviours (Shannon *et al.*, 2018). These zones, when combined with community education and awareness programs, can significantly reduce the likelihood of conflict. Studies have shown that educating communities living near crocodile habitats is an effective strategy in reducing attacks by fostering coexistence between humans and wildlife (Webb & Manolis, 1989).

In addition to habitat protection, active management of crocodile populations, particularly the removal of problematic individuals, must be approached with great caution. While harvest or removal programs have been suggested as a way to address HCC, such measures can disrupt the ecological balance of crocodile populations, particularly in smaller and more isolated river systems. As shown in this study, even small disruptions in demographic structure, such as the removal of key individuals, can lead to sharp declines in survival rates and potential extinction (Allendorf & Hard, 2009).

The introduction of supplementary individuals, especially females, has been proposed as a more sustainable intervention to support population growth (Briggs *et al.*, 2011). However, such interventions must be carefully planned to avoid adverse effects, such as genetic erosion or territorial disputes. Therefore, careful monitoring and assessment of each river system's population dynamics should precede any harvest or supplementation efforts to ensure that the overall conservation goals are met without destabilizing the population (Lacy, 2000).

Another critical management strategy involves facilitating natural migration and gene flow between different river populations of *C. porosus*. As indicated in this study, river systems such as the Kinabatangan show resilience, yet even they face significant challenges due to the lack of genetic diversity. Allowing natural migration between river systems, particularly from genetically richer populations like Paitan, could enhance genetic exchange and strengthen population viability. Studies have demonstrated that promoting gene flow between isolated populations can reduce inbreeding depression and improve the overall adaptability of species (Frankham, 2008). Given the continued use of coastal areas by crocodiles for migration, the establishment of wildlife corridors or safe passage routes along key migration routes could support the movement of individuals and increase genetic diversity in isolated populations.

Finally, addressing the broader issues of habitat degradation and human-wildlife conflict requires a holistic approach that combines conservation efforts with local community involvement. Engaging communities in crocodile conservation initiatives and offering incentives for their active participation can create a more sustainable model for population management. For example, local communities could benefit from ecotourism initiatives centred around crocodile conservation, which can generate funds for further research and management activities. Furthermore, integrating crocodile conservation into regional planning processes that include agriculture and development will help prevent further habitat loss. Sustainable land-use planning that considers both the needs of local communities and the crocodile populations will ensure that the species is preserved for future generations, while minimizing conflict and maximizing coexistence (Campbell *et al.*, 2018).

CHAPTER 6

General Discussion

This thesis offers a comprehensive examination of the ecology, genetics, and conservation management of the estuarine crocodile in Sabah, integrating demographic, genetic, spatial, and population viability perspectives. Through an interdisciplinary approach, the findings underscore the critical role of *C. porosus* as an apex predator and highlight the ecological importance of preserving its populations in Sabah's diverse habitats.

The demographic analysis conducted across 10 rivers in Sabah highlighted substantial variation in the density and size-class structure of *C. porosus* populations, reflecting the complex interplay of ecological and anthropogenic factors influencing their distribution. While *C. porosus* is widely distributed throughout the state, its populations are highly fragmented, with several rivers showing relatively stable densities, whereas others indicate significant declines. This fragmentation is compounded by the discovery of *C. porosus* in rivers where they were previously unrecorded, suggesting shifts in their distribution. Such observations may point to expanding ranges or redistribution due to environmental changes, habitat loss, or the search for more suitable breeding and foraging grounds (Andriyono & Sukistyanawati, 2021).

In addition to population fragmentation, the presence of hatchlings in many surveyed rivers underlines successful breeding and nesting activity in Sabah. Mangroves and swampy areas along these rivers provide optimal habitats for hatchling development, offering refuge and resources for early growth stages (Webb *et al.*, 1983). As noted by Wallace *et al.* (2013) in their study of *C. niloticus* in the Lower Zambezi Valley, a stable crocodile population is typically characterized by a high proportion of juveniles and hatchlings, with fewer large adults. This structure reflects active reproduction and recruitment, critical indicators of population health. The findings from Sabah align with this model, suggesting that certain rivers exhibit promising conditions for *C. porosus* population sustainability. Yet, given the inherently low survival rates of hatchlings, it is essential to minimize disturbances to these fragile environments to support recruitment into older age classes (Webb *et al.*, 2010).

The study also revealed marked differences in population densities across rivers, potentially shaped by habitat quality, prey availability, predation, and human activities (Than *et al.*, 2020). Rivers such as Kinabatangan, Silabukan, and Kalumpang demonstrated relatively healthy crocodile populations, supported by their diverse ecosystems, abundant prey, and minimal human interference. These rivers appear to serve as critical habitats for nesting and growth, maintaining balanced densities across various life stages. In contrast, rivers like Labuk, Segama, Bengkoka, and Padas exhibited lower densities of hatchlings and adults, potentially due to factors such as habitat degradation, high salinity levels, or insufficient prey resources (Ramadani *et al.*, 2023). These findings emphasize the urgent need for conservation measures in areas where populations are struggling, focusing on habitat restoration and reducing anthropogenic pressures.

The spatial movement analysis of *C. porosus* in Sabah provided valuable information on the movement patterns and home range behaviour of this apex predator. Contrary to findings from other studies, the tagged females in this study exhibited larger rates of movement (ROM) on average compared to males. While traditional assumptions suggest that larger individuals typically have larger home ranges, the results from Sabah emphasize the variability in movement patterns within crocodile populations. Females were found to maintain strong fidelity to their core home ranges (Campbell *et al.*, 2013), taking only brief excursions away, while males demonstrated more extensive movement patterns, rarely staying within a defined core area.

One particularly intriguing finding was the observed tendency for some individuals to avoid the vicinity of anthropogenic structures such as the bridge. Although there is no definitive evidence that the Kinabatangan bridge acts as a physical barrier, the data suggests behavioural avoidance in some individuals. For instance, one female established her core home range near the bridge but never crossed under it during the 200+ days she was monitored. This raises concerns about the potential disruption of movement corridors by human infrastructure, which could fragment habitats and alter natural behaviours over time. Such disruptions may have long-term implications for gene flow, access to critical resources, and overall population connectivity (Fukuda *et al.*, 2019; Campbell *et al.*, 2023).

Additionally, the study highlighted the importance of oxbow lakes and tributaries as preferred habitats. These areas often provide essential ecological features, such as calm waters, abundant prey, and suitable basking or nesting sites, making them critical components of the crocodile's habitat (Evans *et al.*, 2016). Conservation efforts should prioritize the protection of these microhabitats, as they play a pivotal role in maintaining healthy crocodile populations (Evan *et al.*, 2017). Ensuring that such habitats remain undisturbed by human activities will be essential for supporting their long-term viability. While the movement study provided valuable data, limitations in technology, such as battery failures, resulted in over 50% data loss, leaving some questions unanswered about long-term movement patterns. Advancements in tagging technology could yield more comprehensive data in future research, providing deeper insights into how *C. porosus* interacts with its environment and navigates anthropogenic challenges (Mascarenhas-Junior *et al.*, 2023).

The genetic analysis of *C. porosus* in Sabah revealed discoveries regarding the population's diversity and structure, providing vital insights for conservation management. While the wild populations overall maintain high genetic diversity, surpassing that of farmed counterparts, this diversity was not evenly distributed among individual river systems. The East Coast populations, in particular, harboured the most genetically diverse individuals, with the Paitan River emerging as a hotspot of genetic diversity. This river's population plays a key role in maintaining the genetic health of *C. porosus* in Sabah and should be prioritized in conservation planning.

Interestingly, individual river populations, with the exception of the Paitan River, displayed relatively low genetic diversity, likely due to limited gene flow and smaller effective population sizes (Castilli-Rodriguez *et al.,* 2024). The presence of more unique haplotypes within rivers, as opposed to shared haplotypes, suggests a degree of genetic isolation among river populations (Haponski & Stepien, 2014). This separation is further reinforced by the distinct haplotypes found on the east and west coasts of Sabah, with no haplotype overlap between these regions. Such differentiation highlights a clear genetic structuring of populations, potentially shaped by geographical barriers and historical environmental changes.

Despite this separation, evidence suggests that some large individuals continue to utilize the sea as a dispersal pathway, maintaining some degree of connectivity between distant populations. For instance, the two problematic crocodiles captured near Kota Kinabalu (West

Coast) provide compelling evidence of long-range coastal movements, with at least one individual potentially originating from the East Coast. This indicates that while populations may be largely isolated, occasional movements via marine routes could contribute to genetic exchange across broader geographic scales (Lloyd- Jones *et al*., 2023). Protecting these rare dispersal events is critical for sustaining genetic flow and enhancing population resilience.

To ensure the long-term viability of *C. porosus* populations in Sabah, conservation strategies must balance the protection of genetically diverse populations, such as those in Paitan, with efforts to bolster genetic diversity in less diverse populations (Panthum *et al.*, 2023). Increasing population sizes through habitat protection and reducing anthropogenic pressures can help support genetic recovery in these rivers. Additionally, fostering connections between isolated populations, potentially through habitat corridors or the preservation of key dispersal pathways, could mitigate the risks of inbreeding and loss of genetic diversity (Gracanin *et al.*, 2023). These efforts will be crucial in maintaining the overall genetic health of *C. porosus* populations across Sabah, ensuring their adaptability and survival in the face of future environmental and anthropogenic challenges.

The Population Viability Analysis (PVA) conducted for *C. porosus* in Sabah provides a critical lens to assess the species' long-term survival under varying environmental and management scenarios. The simulations highlight the significant vulnerability of *C. porosus* populations to habitat loss, reduced genetic diversity, and overharvesting. Despite these challenges, the metapopulation appears capable of surviving the next 100 years, though this persistence is heavily reliant on the Kinabatangan population, highlighting the critical role of the Kinabatangan River as a stronghold for *C. porosus* in Sabah and emphasizes the need for its sustained protection.

Other rivers in Sabah, however, present a rather concerning outlook. The PVA revealed that populations in many rivers are unlikely to remain sustainable over the next century without targeted intervention. Rivers such as Padas and Labuk are particularly at risk, with projections indicating potential population declines or local extinction in the near future. These findings necessitate urgent research into the ecological and anthropogenic factors driving these trends, including habitat degradation, prey availability, and human-crocodile conflicts (HCC) (Kumar *et al*., 2012). By addressing the root causes of these declines, management actions can be better tailored to stabilize and, if possible, reverse these trends.

The simulations also underline the risks associated with harvesting as a potential strategy to mitigate HCC. While controlled harvests may alleviate immediate conflicts, they must be approached with extreme caution to avoid exacerbating population declines. Overharvesting could deplete already fragile populations, particularly in rivers with low densities or those already showing signs of stress. This can also lead to reduced genetic diversity and increased vulnerability to environmental changes (Fukuda *et al.*, 2020). Management plans should prioritize non-lethal methods of conflict mitigation, such as community education, improved livestock management, and habitat modifications, to reduce HCC without compromising population viability.

In conclusion, while the PVA provides a cautiously optimistic outlook for the overall metapopulation of *C. porosus* in Sabah, the findings also serve as a stark reminder of the fragility of individual populations. Protecting the Kinabatangan as a keystone population, coupled with targeted interventions in at-risk rivers like Padas and Labuk, will be pivotal for ensuring the long-term survival of *C. porosus* in Sabah.

These variations highlight the necessity for targeted conservation approaches that account for local ecological conditions and population dynamics. A one-size-fits-all strategy is unlikely to address the diverse challenges facing *C. porosus* populations across Sabah. Developing site-specific management plans that incorporate demographic, genetic, and spatial data will be crucial for effective conservation. As noted by Webb & Smith (1987), understanding population trends requires integrating survival rates, reproductive success, and spatial movements. By combining these demographic insights with spatial analyses, it becomes possible to predict future population shifts and devise strategies to mitigate potential declines.

Habitat restoration should be a top priority, including the rehabilitation of riparian zones, mangroves, and swamps that are critical for nesting and foraging. Protecting these habitats from encroachment or degradation due to agriculture, logging, or urban expansion will help ensure the availability of resources necessary for crocodile survival and reproduction (Veach *et al.*, 2017). These areas are characterized by deeper water, low wave action, and intermediate salinities, providing essential conditions for their survival (Mazzotti & Cherkiss, 2003). Additionally, mangroves act as nurseries for thousands of small fish, many of which spend their adult lives in the ocean. They also stabilize land, creating a buffer against storm surges and hurricane damage (Frost Science, 2023).

Establishing buffer zones along these rivers can mitigate habitat loss and protect nesting sites. Furthermore, human-crocodile conflict (HCC) must be addressed to reduce retaliatory killings, a major driver of population declines (Jeremiah & Reniko, 2018). Community education programs focusing on coexistence strategies, such as securing livestock and managing waste effectively, have shown success in other regions (Wildlife Conservation Action, n.d.; Forestry.com, n.d.). For example, in Sri Lanka, community-based initiatives around *C. porosus* habitats have reduced conflict and fostered coexistence (Wijesundara & Karawita, 2024), which could be similarly applied in Sabah. Additionally, reintroducing captive-bred juveniles from genetically diverse stocks into some rivers could supplement population numbers if monitored carefully to ensure survival and integration.

Facilitating natural gene flow between isolated populations through the establishment of habitat corridors or the restoration of degraded pathways is critical (Free Science, n.d.). If natural connectivity is impractical, translocation programs can be considered, where individuals from genetically diverse populations, such as those in the Paitan River, are introduced into low-diversity populations. However, such programs should be informed by genetic assessments to ensure compatibility and avoid disrupting local adaptations. Collaborative research with geneticists is essential for designing and monitoring these interventions, ensuring their long-term success and minimizing unintended ecological consequences.

The impact of anthropogenic structures, such as bridges and dams, on crocodile movement must also be carefully monitored. Long-term telemetry studies using improved GPS tracking technology can help map movement patterns and identify potential barriers (Mascarenhas-Junior *et al.*, 2023). Observations from the Kinabatangan River, where some individuals avoid swimming under bridges, suggest behavioural disruptions that could impede habitat connectivity and resource access. Mitigation strategies, such as designing wildlife-friendly infrastructure or creating bypasses, should be explored. Additionally, developing artificial wetlands or oxbow lakes near these structures could provide alternative habitats and reduce the need for individuals to traverse disruptive areas.

Involving local communities in monitoring efforts could enhance conservation outcomes. Citizen science initiatives, such as reporting crocodile sightings and movements near bridges or other structures, can provide valuable supplementary data while fostering local engagement in conservation efforts (Crocodile Research Coalition, n.d.; Crocodile Count, n.d.). By integrating these targeted strategies, it is possible to address population recovery, enhance genetic diversity, and mitigate movement challenges, ensuring the resilience of *C. porosus* populations in Sabah over the long term.

CHAPTER 7

Conclusion

In conclusion, this study highlights the importance of adopting a balanced and comprehensive approach to the conservation of *C. porosus* populations in Sabah. Vulnerable populations, particularly those in rivers at risk of decline, must be prioritized, while healthier populations should be safeguarded to ensure their continued stability. Efforts should focus on preserving critical habitats, maintaining ecological integrity, and addressing key threats such as habitat degradation, human-crocodile conflict, and genetic isolation. Promoting coexistence between humans and crocodiles is essential, requiring targeted management strategies and community involvement to achieve sustainable conservation outcomes.

This thesis provides a holistic exploration of the ecology, genetics, movement, and viability of *C. porosus* populations, offering insights that emphasize the interconnectedness of these factors in shaping the species' survival. The findings demonstrate both the strengths of Sabah's crocodile populations, such as high genetic diversity and evidence of successful reproduction, and their vulnerabilities, including population fragmentation and anthropogenic pressures. By integrating demographic, genetic, spatial, and viability analyses, this research underscores the need for conservation strategies that are adaptive and grounded in scientific evidence.

As human development and environmental changes continue to exert pressure on natural ecosystems, ensuring the survival of *C. porosus* as a keystone species is crucial for maintaining ecological balance and biodiversity in Sabah. This thesis emphasizes the urgent need for proactive, science-based management to secure a future where *C. porosus* continues to thrive as an integral part of Sabah's natural heritage.

References

Adame, M. F., Jardine, T. D., Fry, B., Valdez, D., Lindner, G., Nadji, J. and Bunn, S. E. (2018). Estuarine Crocodiles in a Tropical Coastal Floodplain Obtain Nutrition from Terrestrial Prey. *PLoS ONE 13(6):* e0197159.

Aiyer, A., Shine, R. & Somaweera, R. (2022). Shifts in the foraging tactics of crocodiles following invasion by toxic prey. *Scientific Reports*, 12:1267.

Akçakaya, H. R. & Sjögren-Gulve, P. (2000). Population viability analysis for conservation: The importance of demographic and environmental factors. *Conservation Biology*, 14(4), 982-992.

Allendorf, F. W. & Hard, J. J. (2009). Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences*, 106 (Supplement 1), 9987-9994.

Allendorf, F. W. & Luikart, G. (2007). Conservation and the genetics of populations. Blackwell Publishing.

Allendorf, F. W. & Ryman, N. (2002). The role of genetics in the management of the endangered species. *Conservation Biology*, 16(6), 1499-1512.

Amos, W. and Balmford, A. 2001. When does Conservation Genetics matter? *Heredity* 87: 589-596.

Ancrenaz, M., Calaque, R., & Lackman-Ancrenaz, I. (2004). Orangutan nesting behavior in disturbed forest of Sabah, Malaysia: Implications for nest census. *International Journal of Primatology, 25*(5), 983–1000.

Andersen, L. H., Sunde, P., Pellegrino, I., Loechcke, V., Pertoldi, C. Using population viability analysis, genomics, and habitat suitability to forecast future population patterns of little owl (*Athene noctua*) across Europe. 2017. *Ecol Evol*, 7, 10987–11001.

Andriyono, S. & Sukistyanawati, A. (2021). New record of Saltwater crocodile (*Crocodylus porosus*) from East Coast mangrove ecosystem in Surabaya, East Jawa, Indonesia. *Journal of Aquaculture Science*, 6(2):110

Aust, P., Boyle, B., Fergusson, R., & Coulson, T. (2009). The impact of Nile crocodiles on rural livelihoods in northeastern Namibia. *South African Journal of Wildlife Research*, 39(1), 57–69.

Avise JC. 2004. Molecular markers, natural history, and evolution. 2nd ed. Sunderland, Mass: Sinauer Associates.

Avise, J. C. (1994). *Molecular Markers, Natural History and Evolution*. Chapman & Hall.

Avise, J. C. (2000). *Phylogeography: The History and Formation of Species*. Harvard University Press.

Avise, J. C., Arnold, J., Ball, R. M., Bermingham, E., Lamb, T., Neigel, J. E., & Saunders, N. C. (1987). Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, 18, 489-522.

Aziz, M. A., & Islam, M. A. (2018). Population status and spatial distribution of saltwater crocodile, *Crocodylus porosus* in the Sundarbans of Bangladesh. *Bangladesh Journal of Zoology*, *46* (1), 33-44.

Baird, N. A., Etter, P. D., Atwood, T. S., Currey, M. C., Shiver, A. L., Lewis, Z. A., 2008. Rapid SNP Discovery and Genetic Mapping Using Sequenced RAD Markers. *PLoS ONE* 3(10): e3376.

Balmford, A., Mace, G. M. & Ginsberg, J. R. (2001). *Conservation in a Changing World*. Cambridge University Press.

Bandelt, H. J., Foster, P., and Rohl, A. 1999. Median-joining networks for inferring Intraspecific Phylogenies. *Molecular Biology and Evolution*, Volume 16, Issue 1, Pages 37–48.

Banks, E. (2005). *Crocodiles in Borneo*. Natural History Publications.

Barrios-Quiroz, G. & Cremieux, J. (2018). Crocodilian management in Mexico: History and achievements. *Crocodile Specialist Group Newsletter*, *37(3)*, 12-19.

Bayliss, P. (1987). Survey Methods & Monitoring within Crocodile Management Programmes. In: Wildlife Management: Crocodiles and Alligators (Manolis, C., Webb, G.J.W. & Whitehead, P.J.P., eds), Sydney: Survey Beatty & Sons (in Association with the Conservation Commission of the Northern Territory):157-175.

Bayliss, P., Webb, G. J. W., Whitehead, P. J., Dempsey, K. and Smith, A. (1986). Estimating the Abundance of Saltwater Crocodiles, *Crocodylus porosus* Schneider, in Tidal Wetlands of the Northern Territory – A Mark-recapture Experiment to Correct Spotlight Counts to Absolute Numbers, and the Calibration of Helicopter and Spotlight Count. *Australian Wildlife Research 13 (2)*, 309-320.

Bennett, N. J., Di Franco, A., Calò, A., Nethery, E., Niccolini, F., Milazzo, M., & Guidetti, P. (2017). Local support for conservation is associated with perceptions of good governance, social impacts, and ecological effectiveness. *Conservation Letters*, 12(3), e12640.

Berkes, F. (2004). Rethinking community-based conservation. *Conservation Biology*, 18(3), 621-630.

Bezuijen, M. R., Cox, J. H., & Phothitay, C. (2013). Siamese crocodile *Crocodylus siamensis* surveys in Cambodia, Laos, and Vietnam. *Crocodile Specialist Group Newsletter*, *32(2):* 16-19.

Bhaskar, R. & Sharon, D. (2022). Anthropogenic impacts on wildlife populations: A genetic perspective. *Conservation Genetics*, 23, 457-468.

BiologyInsights Team. (2024, August 3). *Apex predators and their crucial role in ecosystem balance*. Biology Insights. Retrieved from https://www.biologyinsights.com

BirdLife International. (2003). *Saving Asia's threatened birds: A guide for government and civil society*. BirdLife International.

Biscarini, F. Cozzi, P. and Orozco-Terwengel, P. 2018. Lessons learnt on the Analysis of Large Sequence Data in Animal Genomics. *Animal Genetics*, Volume 49, Issue3, Pages 147-158.

Bloor, P., Ibanez, C. and Viloria-Lagares, T. A., 2014. Mitochondrial DNA analysis reveals hidden Genetic Diversity of the captive populations of the threatened American Crocodile (*Crocodylus acutus*) in Colombia. *Ecology and Evolution* 5(1): 130-140.

Boonratana, R. (2000). Ranging behaviour of proboscis monkeys (*Nasalis larvatus*) in the Lower Kinabatangan, Northern Borneo. *International Journal of Primatology, 21*(3), 497–518.

Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., Maio, N. Di, Matschiner, M., Mendes, F. K., Müller, N. F., Ogilvie, H. A., Du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I. and Drummond, A. J. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology, 15*(4), e1006650.

Bowen, B. W., Clark, A. M., Abreu-Grobois, F. A., Chaves, A., Reichart, H. A., & Ferl, R. J. (1998). Global phylogeography of the ridley sea turtles (*Lepidochelys spp.*) as inferred from mitochondrial DNA sequences. *Genetica*, 101(3), 179–189.

Brazaitis, P. (1974). The identification of living crocodilians. *Zoologica; scientific contributions of the New York Zoological Society*, 58(3-4), 59-101.

Brien, M. L., Read, M. A., & Grigg, G. C. (2017). "Crocodilians and climate change: Adaptations to environmental challenges." In G. J. W. Webb, S. C. Manolis, & P. J. Whitehead (Eds.), *Crocodiles: Proceedings of the 25th Working Meeting of the Crocodile Specialist Group* (pp. 123–130). IUCN.

Brien, M. L., Webb, G. J. W. & Manolis, S. C. (2014). Crocodilian management and conservation in Australia: Successes and challenges. *Australian Journal of Zoology*, 62(1), 40-53.

Brien, M. L., Webb, G. J. W., & Manolis, S. C. (2008). A method for attaching tracking devices to crocodilians. *Herpetological Review*, 39(3), 302–303.

Brien, M. L., Webb, G. J. W., Manolis, S. C., & Christian, K. A. (2018). The ecological importance of crocodiles in ecosystems. *Biological Conservation*, 227, 26-35.

Briggs, L. D., Johnson, W. E. & Marshall, D. C. (2011). Reintroducing individuals into declining populations: A review and practical guide. *Conservation Biology*, 25(4), 702-710.

Brito, J. C., Godinho, R., Martínez-Freiría, F., Pleguezuelos, J. M., Rebelo, H., Santos, X., Vale, C. G., Velo-Antón, G., Boratyński, Z., Carvalho, S. B., Ferreira, S., Silva, T. L., Tarroso, P., Campos, J. C., Leite, J. V., Nogueira, J., Álvares, F., Sillero, N., & Sow, A. S. (2014). Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. *Biological Reviews*, 89(1), 215–231.

Britton, A. (2012). *Crocodiles: World's top predator*. New Holland Publishers.

Brochu, C. A. (2003). Phylogenetic approaches toward crocodylian history. *Annual Review of Earth and Planetary Sciences*, 31, 357-397.

Brook, B. W. & Bradshaw, C. J. A. (2006). Population viability analysis: A review of the literature and its application to biodiversity conservation. *Biological Conservation,* 130(3), 372-384.

Brooks, J. S., Waylen, K. A., & Mulder, M. B. (2013). How national context, project design, and local community characteristics influence success in community-based conservation projects. *Proceedings of the National Academy of Sciences*, 110(52), 20637-20642.

Brooks, T. M., Mittermeier, R. A., da Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F. & Rodrigues, A. S. L. (2006). Global biodiversity conservation priorities. *Science*, 313(5783), 58-61.

Burgess, M. G., et al. (2019). "Protecting marine mammals, turtles, and birds by rebuilding global fishery populations." *Science,* 365(6452), 645–648.

Burgess, M. M., Nagle, V., & Tuan, D. (2019). Trap shyness in Crocodylus porosus: Implications for conservation and management. *Wildlife Research,* 46(1), 55-65.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24(3), 346–352.

Caldicott, D. G. E., Croser, D., Manolis, C., Webb, G. & Britton, A. (2005). Crocodile attack in Australia: An analysis of its incidence and review of the pathology and management of crocodilian attacks in general. *Wilderness & Environmental Medicine*, 16(3), 143-159.

Calvelrey, P. & Downs, C. T. (2015). Movement and home range of Nile Crocodiles in Ndumo Game Reserve, South Africa. *Area Conservation and Science,* 57(1):1-13.

Campbell, H. A., Dwyer, R. G., Gordos, M. A., & Franklin, C. E. (2015). Aquatic animal tracking through a cost-effective open-source platform. *Methods in Ecology and Evolution*, *6(4):* 447-456.

Campbell, H. A., Dwyer, R. G., Gordos, M. A., Franklin, C. E. (2015). Aquatic animal tracking through a cost-effective open-source platform. *Methods in Ecology and Evolution*, 6(4), 447-456.

Campbell, H. A., Dwyer, R. G., Irwin, T. R., and Franklin, C. E. 2013. Home Range Utilization and long-range Movement of Estuarine Crocodiles during the breeding and nesting season. *PLoS ONE* 8(5): e62127.

Campbell, H. A., Dwyer, R. G., Wilson, H., & Franklin, C. E. (2013). Home range utilisation and long-range movement of estuarine crocodiles during the breeding and nesting season. *PLOS ONE,* 8(5), e62127.

Campbell, H. A., Sullivan, S., Read, M. A. & Franklin, C. E. (2013). Ecological and environmental factors influencing the movement patterns of estuarine crocodiles (*Crocodylus porosus*) in a highly urbanized area. *PLoS ONE*, 8(8), e71179.

Campbell, H. A., Watts, M. E., Sullivan, S., Read, M. A., Choukroun, S., Irwin, S. R., & Franklin, C. E. (2010). Estuarine crocodiles ride surface currents to facilitate long-distance travel. *Journal of Animal Ecology*, 79(5), 955-964.

Campbell, H. A., Watts, M. E., Sullivan, S., Read, M. A., Choukroun, S., Irwin, Steve. R. and Franklin, C. E. 2010. Estuarine Crocodiles ride surface currents to facilitate long-distance travel. *Journal of Animal Ecology*: Vol 79, Issue 5: 955-964.

Campbell, H. W. (1973). Ecological and behavioral relationships of *Caiman crocodilus* and *Melanosuchus niger* in South America. *Herpetologica*, 29(1), 1-6.

Campbell, S. J., Fitzsimons, J. A. & Webb, G. J. W. (2018). Conservation and management of crocodiles: Challenges and strategies. *Journal of Wildlife Management*, 82(6), 1209-1222.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J. & Mace, G. M. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, 309(5738), 1239-1241.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P. & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature, 486(7401):* 59-67.

Castillo-Rodriguez, N., Saldarriaga-Gomez, A. M., Antelo, R. & Vargas-Ramirez, M. (2024). First genetic evaluation of a wild population of *Crocodylus intermedius*: new insights for the recovery of a critically endangered species. *PLoS ONE,* 19(10).

Caswell, H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*. 2nd ed. Sinauer Associates.

Cegelski, C. C., Waits, L. P., & Anderson, N. J. (2006). Assessing population structure and gene flow in Montana wolverines (*Gulo gulo*) using assignment-based approaches. *Molecular Ecology*, 15(11), 3251–3260.

Chabreck, R. H. (1979). The marshes of Louisiana: A resource and their management. New Orleans: Louisiana State University Press.

Charruau, P., Rissac, A. & Diaz, D. A. M. (2021). A new case of communal egg-laying by iguanas and American crocodiles (*Crocodylus acutus* Cuvier, 1807) from a Caribbean atoll of Mexico. *Caribbean Herpetology* 80, 1-5.

Chediack, D. (2009). Sustainable wildlife management: integrating ecological monitoring with policy formation. *Biodiversity and Conservation*, *18,* 1345-1357.

Cicero, C., & Johnson, N. K. (1998). Molecular phylogeny and ecological diversification in a clade of New World songbirds (genus *Vireo*). *Molecular Ecology, 7*(10), 1359–1370.

CITES. (2021). "The CITES Appendices." *Convention on International Trade in Endangered Species of Wild Fauna and Flora*.

Coleman, T. S., Gabel, W., Easter, M., McGreal, M., Marin, M. S., Garrigos, D. B., Murray, & C. M. (2024). The Spatial Ecology of Nuisance Crocodiles: Movement Patterns of Relocated American Crocodiles (*Crocodylus acutus*) in Guanacaste, Costa Rica. *Animals*, 14, 339.

Combrink, X. (2015). "Spatial and reproductive ecology of the Nile crocodile (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa." [Doctoral dissertation, University of KwaZulu-Natal].

Cotroneo, L. A. 2010. Population genetics and conservation of the American crocodile on the Pacific Coast of Costa Rica. *PhD Thesis, Drexel University*.

Cott, B. (2010). Crocodiles: Biology, husbandry and diseases. *Journal of Herpetology,* 44(2), 256–257.

Cott, H. B. (1961). Scientific Results of an Inquiry into the Ecology and Economic Status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Trans. Zool. Soc. London 29*: 211-356.

Cox, J. & Gombek, F. (1985). A Preliminary Survey of the Crocodile Resources in Sarawak, East Malaysia., ICUN/ WWF Project No. MAL 74/85. WWF, Kuala Lumpur.

Cox, J. (1985). Crocodile management in Papua New Guinea: Policy and practice. *Conservation Biology*, 1(1), 13-17.

Crocodile Count. (n.d.). *Charotar Crocodile Count: Monitoring and conservation of mugger crocodiles*. Retrieved from https://crocodilecount.org.

Crocodile Research Coalition. (n.d.). *Biodiversity surveys and community engagement programs*. Retrieved from https://crocodileresearchcoalition.org/biodiversity-surveys.

Crocodile Specialist Group. (1989). *Crocodiles: Their ecology, management, and conservation*. A special publication of the Species Survival Commission of the International Union for Conservation of Nature and Natural Resources. IUCN.

Cushman, S. A. & Huettmann, F. (2010). *Spatial Complexity, Informatics, and Wildlife Conservation*. Springer Science & Business Media.

Davey, J. L., and Blaxter, M. W. 2010. RADSeq: Next-generation Population Genetics. *Briefings in Functional Genomics* 9: 416–423.

Dawson, M. N., Raskoff, K. A., & Jacobs, D. K. (2001). Field preservation of marine invertebrate tissue for DNA analyses. *Molecular Marine Biology and Biotechnology, 10*(1–2), 37–52.

De Jesús-Crespo, R., Jha, M., & Chaves-Campos, J. (2019). Genetic differentiation and adaptation in American alligator (*Alligator mississippiensis*) populations across riverine systems. *Herpetological Conservation and Biology*, 14(2), 212-224.

Delany, M. F. &. Abercrombie, C. L. (1986). American Alligator Food Habits in North Central Florida. *J. Wildlife. Manage. 50:(2)*348-353.

Dever, J. A., Strauss, R. E., Rainwater, T. R., McMurry, S. T., Densmore, L. D., 2002. Genetic diversity, population subdivision and gene flow in Morelet’s Crocodile (*Crocodylus moreletii*) from Belize, Central America. *Copeia* 2000:1078–1091.

Dickman, A. J. (2010). Complexities of conflict: The importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation*, 13(5), 458-466.

Dinets, V., Brueggen, J., & Brueggen, J. C. (2013). Crocodilian attack incidents on humans in the United States. *Human Dimensions of Wildlife*, 18(6), 461-468.

Drummond, A. J., Rambaut, A., Shapiro, B., & Pybus, O. G. (2005). Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*, 22(5), 1185–1192.

Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., and White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife*, 3, e00590.

Dutton, P. H., Roden, S. E., Stewart, K. R., LaCasella, E., Tiwari, M., Formia, A., Thomé, J. C., Livingstone, S. R., Eckert, S., Chacon-Chaverri, D., Rivalan, P., & Allman, P. (2013). Population structure, phylogeography and genetic diversity of leatherback turtles (*Dermochelys coriacea*). *Journal of Zoology*, 291(4), 313–320.

Eaton, P. (2010). Dams, nation, and the colonial enterprise: The case of Manipur's Loktak Lake. *Geoforum, 41*(6), 877–885.

Encyclopaedia Britannica. (2024). *Encyclopaedia Britannica* (15th ed.).

Erickson, G. M., Gignac, P. M., Steppan, S. J., Lappin, A. K., Vliet, K. A., Brueggen, J. D. & Inouye, B. D. (2012). Insights into the ecology and evolutionary success of crocodilians revealed through bite-force and tooth-pressure experimentation. *PLOS ONE*, 7(3), e31781.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J. & Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, *333(6040):* 301-306.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M. E., Virtanen, R., & Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, *333*(6040), 301–306.

Evans, J. E., Jones, T. H., Pang, K., Saimin, S. & Goossens, B. (2016). Spatial ecology of Estuarine crocodiles (*Crocodylus porosus*) nesting in a fragmented landscape. *Sensors,* 16, 1527.

Evans, L. J., Davies, A. B., Goossens, B. and Asner, G. P. (2017). Riparian Vegetation Structure and the Hunting Behavior of Adult Estuarine Crocodiles. *PLoS ONE, 12 (10)*, e0184804.

Excoffier, L and Lischer, H. E. L., 2010. Arlequin Suit ver 3.5: A new series of programs to perform Population Genetics analysis under Linux and Windows.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487–515.

Fergusson, R.A. (2010). Nile Crocodile *Crocodylus niloticus*. Crocodiles: Status Survey and Conservation Action Plan. Third Edition, ed. by S.C. Manolis and C. Stevenson. Crocodile Specialist Group: Darwin. Pp. 84-89.

FitzSimmons, N. N., Buchan, J. C., Lam, P. V., Polet, G., Hung, T. T., Thang, N. Q., & Gratten, J. (2001). Identification of purebred Crocodylus siamensis for reintroduction in Vietnam. *Journal of Experimental Zoology*, 294(4), 373–379.

Fitzsimmons, N., Buchan, J., and Lam, P. 2002. Identification of purebred *Crocodylus siamensis* for reintroduction in Vietnam. *Mol. Dev. Evol.* 294:373–381.

Forestry.com. (n.d.). *Navigating human-wildlife conflict: Community-based approaches to coexistence*. Retrieved from https://forestry.com/wildlife-management/human-wildlife-interaction/navigating-human-wildlife-conflict/.

Frankham, R. (1996). Relationship of genetic variation to population size in wildlife. *Conservation Biology*, 10(6), 1500-1508.

Frankham, R. (2005). Genetics and extinction. *Biological Conservation,* 126(2), 131-140.

Frankham, R. (2008). Genetic adaptation to captivity in species conservation programs. *Molecular Ecology,* 14(8), 1851-1871.

Free Science. (n.d.). *Wildlife corridors: Facilitating species movement and genetic flow.* Retrieved from https://freescience.info/wildlife-corridors-facilitating-species-movement-and-genetic-flow.

Frost Science. (2023). Local crocodiles hatch amid mangroves, highlighting relevance of our Frost Science mangrove habitat. Retrieved from: https://www.frostscience.org/local-crocodiles-hatch-amid-mangroves-highlighting-relevance-of-our-frost-science-mangrove-habitat/.

Fujisaki, I., Hart, K. M., Massotti, F. J., Cherkiss, M. S., Sartain, A. R., Jeffery, B. M, Beauchamp, J. S. &Denton, M. (2014). *Animal Biotelemetry,* 2:8

Fujisaki, I., Mazzotti, F. J., Dorazio, R. M., Rice, K. G., Cherkiss, M. S., & Jeffery, B. M. (2011). Estimating trends in alligator populations from nightlight survey data: A Bayesian approach. *Wetlands*, *31(6):* 1303-1312.

Fukuda, Y. & Cuff, N. (2013). *Crocodylus porosus* (Saltwater Crocodile) Nesting. *Herpetological Review, 44(3):* 500-501.

Fukuda, Y. & Cuff, N. (2013). Vegetation Communities as Nesting Habitat for the Saltwater Crocodiles in the Northern Territory of Australia. *Herpetological Conservation and Biology, 8 (3)*: 641-651.

Fukuda, Y., Manolis, C., & Appel, K. (2014). Management of human–crocodile conflict in the Northern Territory, Australia: Review of crocodile attacks and removal of problem crocodiles. *The Journal of Wildlife Management,* 78(7), 1239–1249.

Fukuda, Y., Manolis, S. C. & Appelton, B. (2013). Saltwater crocodile (*Crocodylus porosus*) management in the Northern Territory, Australia: 2009–2012. *Northern Territory Naturalist, 24:* 14–29.

Fukuda, Y., Manolis, S. C. & Appelton, B. (2014). Management of human-crocodile conflict in the Northern Territory of Australia: Review of crocodile attacks and removal program. *Journal of Wildlife Management*, *78(7):* 1239-1249.

Fukuda, Y., Saalfeld, K., & Webb, G. (2013). "Standardised method of spotlight surveys for crocodiles in the tidal rivers of the Northern Territory, Australia." *Northern Territory Naturalist,* 24, 14–32.

Fukuda, Y., Webb, G. J. W., Manolis, S. C., & Saalfeld, K. (2019). The management of saltwater crocodiles in the Northern Territory, Australia: A success story of sustainable use. *Journal of Wildlife Management*, 83(5), 1387-1395.

Fukuda, Y., Webb, G. J. W., Manolis, S. C., Delaney, R., Letnic, M., Linder, M. and Whitehead, P. J. (2011). Recovery of Saltwater Crocodiles Following Unregulated Hunting in Tidal Rivers of the Northern Territory, Australia. *Journal of Wildlife Management, 75 (6),* 1253-1266.

Fukuda, Y., Webb, G. J., Manolis, S. C. & Saalfeld, K. (2014). Broad-scale environmental influences on the distribution and abundance of saltwater crocodiles (*Crocodylus porosus*) in Northern Australia. *Wildlife Research*, *41(2)*, 131-143.

Fukuda, Y., Webb, G. J., Manolis, S. C. & Saalfeld, K. (2019). The management of saltwater crocodiles in the Northern Territory, Australia: A success story of sustainable use. *Journal of Wildlife Management*, *83(5),* 1387-1395.

Fukuda, Y., Webb, G., Manolis, C. & Saalfeld, K. (2019). "The management of saltwater crocodiles in the Northern Territory, Australia: A success story of sustainable use." *Journal of Wildlife Management, 83(5):* 1387-1395.

Fukuda, Y., Webb, G., Manolis, C., Saalfeld, K., & Risk, R. (2013). Standardised method of spotlight surveys for crocodiles in the tidal rivers of the Northern Territory, Australia. *Northern Territory Naturalist*, *24*: 14-32.

Fukuda, Y., Whitehead, P. and Boggs, G. (2007). Corrigendum to: Broad-scale Environmental Influences on the Abundance of Saltwater Crocodiles (*Crocodyus porosus*) in Australia. *Wildlife Research, 34,* 160-176.

Gaillard, J. M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Van Moorter, B. (2010). Habitat-performance relationships: Finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365(1550),* 2255-2265.

Galezo, A. A., Mann, J., Ritchie, B., & Krzyszczyk, E. (2017). Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. *Behavioral Ecology, 28*(2), 362–371.

Games, I., Blake, D. K., & Loveridge, J. P. (1992). Crocodile Numbers on Lake Kariba, Zimbabwe, and Factors Influencing them. Proceedings of the 11th Working Meeting of the Crocodile Specialist Group of the Species Survival Commission of the IUCN, Vol. 2, pp. 163–175.

Garcia-Grajales, J., Briseno, R., & Rivera, A. (2007). Population ecology and conservation of *Crocodylus acutus* in a coastal area of Oaxaca, Mexico. *Herpetological Conservation and Biology*, 2(1), 11-17.

Gaston, K. J. & Fuller, R. A. (2008). Commonness, population depletion, and conservation biology. *Trends in Ecology & Evolution*, *23(1)*, 14-19.

Gilpin, M. E. & Soulé, M. E. (1986). Minimum viable populations: Processes of species extinction. In M. E. Soulé (Ed.), *Conservation Biology: The Science of Scarcity and Diversity* (pp. 19–34). Sinauer Associates.

Giri, C., Ochieng, E., Tieszen, L. L., Zhu, Z., Singh, A., Loveland, T., Masek, J. & Duke, N. (2011). Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography*, *20(1)*: 154-159.

Glenn, T. C., Staton, J. L., Vu, A. T., Davis, L. M., Alvarado Bremer, J. R., Rhodes, W. E., and Sawyer, R. H., 2002. Low mitochondrial DNA variation among American alligators and a novel non-coding region in crocodilians. *Journal of Experimental Zoology*, *294*(4), 312–324.

Gonzalez, J. A., Bechara, A. E., & Quintana, D. (2019). Spatial ecology and conservation of *Crocodylus intermedius* in Venezuela. *Biological Conservation,* 238, 108210.

González-Trujillo, R., Rodriguez, D., and González-Romero, A. 2012. Testing for hybridization and assessing genetic diversity in Morelet's crocodile (*Crocodylus moreletii*) populations from central Veracruz. *Conservation Genetics*, 13, 1677-1683.

Gotelli, N. J. (2001). *A Primer of Ecology*. 3rd ed. Sinauer Associates.

Gracanin, A., Knipler, M. L. & Mikac, K. M. (2023). Informing wildlife corridor creation through population genetics of an arboreal marsupial in a fragmented landscape. *Genes*, *14*(2), 349.

Graham, A. (1968). The Lake Rudolf Crocodile (*Crocodylus niloticus* Laurenti) Population. Unpublished. Master's thesis, Univ. of Nairobi, Nairobi, Kenya.

Gratten, J. 2003. The Molecular Systematics, Phylogeography and Population Genetics of Indo-Pacific Crocodylus. *PhD Thesis, University of Queensland*.

Green, R. E., Braun, E. L., Armstrong, J., Earl, D., Nguyen, N., Hickey, G., & Wilson, R. K. (2014). Three crocodilian genomes reveal ancestral patterns of evolution among archosaurs. *Science*, 346(6215), 1254449.

Grigg G. C., Taplin L. E., Harlow P., and Wright J. (1980) Survival and Growth of Hatchling *Crocodylus porosus* in Saltwater without Access to Fresh Drinking Water. *Oecologia 47*, 264-266.

Grigg, G. & Kirshner, D. (2015). *Biology and Evolution of Crocodylians*. CSIRO Publishing.

Grigg, G. C. (1981). Plasma Homeostasis and Cloacal Urine Composition in *Crocodylus porosus* Caught along a Salinity Gradient. *J. Comp. Physiol. 144*:261-270.

Grigg, G. C., Kirshner, D. S., & Seebacher, F. (2001). Crocodile morphophysiology and behavior: Adaptations and comparisons with other vertebrates. *Journal of Comparative Physiology*, 171(3), 287-300.

Grigg, G., & Kirshner, D. (2007). *Biology and evolution of crocodylians*. Cornell University Press.

Grigg, G., & Kirshner, D. (2015). *Biology and Evolution of Crocodylians*. CSIRO Publishing.

Groombridge, B. (1987). The distribution and status of world crocodilians. In G. J. W. Webb, S. C. Manolis, & P. J. Whitehead (Eds.), *Wildlife Management: Crocodiles and Alligators* (pp. 9–21). Surrey Beatty & Sons Pty Limited.

Grumbine, R. E. (1994). What is ecosystem management? *Conservation Biology*, 8(1), 27-38.

Hanski, I. (1999). *Metapopulation Ecology*. Oxford University Press.

Haponski, A. E. & Stepien, C. A. (2014). A population genetic window into the past and future of the walleye *Sander vitreus*: relation to historic walleye and the extinct "blue pike" *S. v. "glaucus". BMC Evolutionary Biology,* 14(133).

Harpending, H. C. (1994). Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. *Human Biology, 66*(4), 591–600.

Harris, S., Cresswell, W. J., Forde, P. G., Trewhella, W. J., Woollard, T., & Wray, S. (1990). Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review,* 20(2–3), 97–123.

Harrison, R. G. (1989). Animal mitochondrial DNA as a genetic marker in population and evolutionary biology. *Trends in Ecology & Evolution*, 4(1), 6-11.

Harrison, R. G. (1989). Animal mitochondrial DNA as a genetic marker in population and evolutionary biology. *Trends in Ecology & Evolution, 4*(1), 6–11.

Hasegawa, M., Kishino, H., & Yano, T. (1985). Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution, 22*(2), 160–174.

Hay, J. M., Sarre, S. D., Lambert, D. M., Allendorf, F. W., & Daugherty, C. H. (2010). Genetic diversity and taxonomy: A reassessment of species designation in tuatara (*Sphenodon*) using mitochondrial DNA phylogenetics. *Conservation Genetics*, 11(3), 1063–1081.

Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., and Sequeira, A. M. M. (2016). Translating marine animal tracking data into conservation policy and management. *Trends in Ecology & Evolution*, 31(2), 77–87.

Hekkala, E. R., Amato, G., DeSalle, R., & Blum, M. J. (2010). Molecular assessment of population differentiation and individual assignment potential of Nile crocodile (*Crocodylus niloticus*) populations. *Conservation Genetics*, 11(4), 1435–1443.

Hekkala, E., Shirley, M. H., Amato, G., Austin, J. D., Charter, S., Thorbjarnarson, J., Vliet, K. A., Houck, M. L., Desalle, R., & Blum, M. J. (2011). Global phylogeny of *Crocodylus* (Crocodylia) and the evolutionary history of American crocodiles. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 316(5), 466-472.

Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, 142(1), 14-32.

Hengeveld, R. (1993). What to do about the North American invasion by the collared dove? *Journal of Field Ornithology*, 64(4), 477–489.

Hockings, M., Stolton, S., Leverington, F., Dudley, N., & Courrau, J. (2015). *Evaluating Effectiveness: A Framework for Assessing the Management of Protected Areas*. IUCN.

Hohenlohe, P. A., Funk, W. C. & Rajora, O. P. (2021). Population genomics for wildlife conservation and management. *Evolutionary Applications*, 14(1), 235-246.

Hollands, M. (1987). Crocodile conservation in Papua New Guinea. *WWF Conservation Reports*.

Holsinger, K. E., & Weir, B. S. (2009). Genetics in geographically structured populations: Defining, estimating, and interpreting FST. *Nature Reviews Genetics, 10*(9), 639–650.

Hughes, A. C. (2017). Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere*, 8(1), e01624.

Hughes, J. M., Schmidt, D. J., & Finn, D. S. (2009). Genes in streams: Using DNA to understand the movement of freshwater fauna and their riverine habitat. *BioScience*, 59(7), 573–583.

Hunter, L. T., White, P., Henschel, P., Frank, L., & Burton, C. (2010). Walking with lions: Why there is no role for captive-origin lions in species restoration. *Oryx*, 46(2), 185-193.

Hutton, J. M. (1987). Growth and survival of the Nile crocodile (*Crocodylus niloticus*) in Lake Ngezi, Zimbabwe. *Journal of Animal Ecology*, 56(1), 25-38.

Hutton, J. M., & Webb, G. J. W. (1992). An introduction to the farming of crocodilians. *Proceedings of the 11th Working Meeting of the IUCN Crocodile Specialist Group*. IUCN.

Hutton, J. M., & Woolhouse, M. E. (1989). Mark-recapture to assess factors affecting the proportion of a Nile crocodile population seen during spotlight surveys. *Journal of Applied Ecology*, *26(2):* 381-395.

Ibrahim, H., Zahari, Z. & Hazmi, R. (2010). Human-crocodile interactions in Sarawak. *Sarawak Museum Journal*, 67, 145-152.

Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: A review of patterns and priorities worldwide. *Oryx*, 43(1), 18-34.

IUCN Red List - http://www.iucnredlist.org Accessed on 20th July 2014.

Jalil, M. F. (2016). Distribution and conservation of *Crocodylus porosus* in Kinabatangan River, Sabah, Malaysia. *Journal of Wildlife Research, 24*: 25-32.

Jeremiah, C. & Reniko, G. (2018). The human crocodile conflicts and the sustainable conflict resolutions review. *Int J Environ Sci Nat Res*, 13(2): 555856.

Jensen-Seaman, M. I., & Kidd, K. K. (2001). Mitochondrial DNA variation and biogeography of eastern gorillas. *Molecular Ecology, 10*(9), 2241–2247.

Joanen, T. & McNease, L. (1971). Propagation of the American alligator in captivity. *Proceedings of the Southeastern Association of Game and Fish Commissioners*, 25, 106-116.

Kappeler, P. M. (2019). A framework for studying social complexity. *Behavioral Ecology and Sociobiology, 73,* 13.

Kareiva, P., Tallis, H., Ricketts, T. H., Daily, G. C., & Polasky, S. (2011). *Natural Capital: Theory and Practice of Mapping Ecosystem Services*. Oxford University Press.

Kasim, N. Y. (2012). Genetic diversity of saltwater crocodiles (*Crocodylus porosus*) from Sarawak using microsatellite approach (Master's thesis, Universiti Malaysia Sarawak).

Kay, W. R. (2004). Movements and home ranges of radio-tracked *Crocodylus porosus* in the Cambridge Gulf region of Western Australia. *Wildlife Research*, 31(5), 495–508.

Kays, R., Crofoot, M. C., Jetz, W. & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, 348(6240), aaa2478.

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, 348(6240), 1222-1231.

Kery, M., & Royle, J. A. (2015). *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS*. Academic Press.

King, F. W. (1988). *Crocodiles: An Action Plan for their Conservation*. IUCN/SSC Crocodile Specialist Group. This action plan provides detailed accounts of the conservation status and management programs for crocodile species globally, emphasizing the need for sustainable management strategies for their protection. It was published by the International Union for Conservation of Nature (IUCN).

Klein, D. R., Carr, A. J., & McCarthy, M. A. (2019). Movement ecology of *Crocodylus acutus* in coastal habitats of Florida. *Journal of Herpetology,* 53(1), 83-92.

Klimley, A. P. (2014). "The Biology of Sharks and Rays." *University of Chicago Press*.

Kobilinsky, D. (2019, October 21). Florida panther genome reveals higher genetic diversity. *The Wildlife Society*.

Kramer-Schadt, S., Niedballa, J. & Pilgrim, J. D. (2009). The importance of considering environmental variables in PVA models for conservation planning. *Ecological Applications, 19*(2), 512-524.

Kumar, S. S., Sivaperuman, C. & Yadav, B. P. (2012). Management of problem saltwater crocodiles (*Crocodilus porosus* Schneider) – a case study in the Andaman and Nicobar Islands, India. *Herpetological Bulletin*, 120, 9-15.

Lacy, R. C. (2000). Structure of the Vortex: A computer simulation for population viability analysis. *Ecology*, 81(4), 1530-1541.

Lacy, R. C. (2009). Vortex: A stochastic simulation of the extinction process. *Version 10.0 user manual*. Chicago, IL: Chicago Zoological Society.

Lading, E. (2013). Crocodile attacks in Sarawak. In *Crocodiles: Proceedings of the 22nd Working Meeting of the IUCN-SSC Crocodile Specialist Group* (p. 96). IUCN.

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist, 142*(6), 911-927.

Lang, J. W. (1987). Crocodilian behaviour: Implications for management. In G. J. W. Webb, S. C. Manolis & P. J. Whitehead (Eds.), *Wildlife Management: Crocodiles and Alligators* (pp. 273-294). Surrey Beatty & Sons.

Lang, J. W. (1987). Crocodilian behaviour: Implications for management. In G. J. W. Webb, S. C. Manolis, & P. J. Whitehead (Eds.), *Wildlife Management: Crocodiles and Alligators* (pp. 273–294).

Langton, M. (2008). *The Dreaming & Other Essays: Indigenous Australians & the Social Construction of Reality*. Arena Publications.

Lapbenjakul, S., Thapana, W., Twilprawat, P., Muangmai, N., Kanchanaketu, T. and, Temsiripong, Y. 2017. High Genetic Diversity and Demographic history of captive Siamese and Saltwater crocodiles suggest the first step toward the establishment of a breeding and reintroduction program in Thailand. *PLoS ONE* 12(9): e0184526.

Laurance, W. F., Useche, D. C., Rendeiro, J., Kalka, M., Bradshaw, C. J., Sloan, S. P. & Giam, X. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, 489(7415), 290-294.

Law, R. (2000). Fishing and the evolution of size distributions. *Ecology Letters*, 3(3), 235-240.

Lecocq, T., Brasero, N., Martinet, B., Valterová, I., & Rasmont, P. (2013). Highly polytypic taxon complexes, intra-taxon variability and time-consistent DNA barcoding: insights from *Bombus lapidarius* (Hymenoptera: Apidae). *Systematic Entomology, 38*(4), 723-733. doi:10.1111/syen.12020

Lee, H. A. (2020). Unemployment among Malaysia's Youth: Structural Trends and Current Challenges. *Iseas Perspective, Issue 2020 (65)* 2335-6677.

Leigh, J. W., & Bryant, D. (2015). PopART: Full-feature software for haplotype network construction. *Methods in Ecology and Evolution, 6*(9), 1110–1116.

Letnic, M. & Connors, G. (2006). Changes in the Distribution and Abundance of Saltwater Crocodiles (*Crocodylus porosus*) in the Upstream, Freshwater Reaches of Rivers in the Northern Territory. *Wildlife Research, 33 (7)* 529-538.

Levin, N., Lechner, A. M., Brown, G., & McAlpine, C. A. (2013). An evaluation of crowdsourced information for assessing the spatial distribution of vegetation cover: A case study of Mount Kenya. *PLOS ONE*, 8(7), e67625.

Lewis, D. L., Webb, G. J. W. & Manolis, S. C. (2013). Behavioral thermoregulation and water-use patterns of saltwater crocodiles in the Northern Territory. *Herpetological Conservation and Biology*, 8(2), 95-103.

Librado, P. and Rozas, J. 2009. DnaSP V5: A Software for Comprehensive analysis of DNA Polyorphism data. *Bioinformatics*, Volume 25, Issue 11, 1 June 2009, Pages 1451–1452.

Lima, S. L., & Zollner, P. A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, 11(3), 131–135.

Lindenmayer, D. & Likens, G. E. (2010). Effective ecological monitoring. *Earthscan*.

Lindenmayer, D. (2016). Interactions between forest resource management and landscape structure. *Curr Landscape Ecol Rep,* 1:10–18

Llobet, A., & Seijas, A. E. (2003). Population ecology of *Caiman crocodilus* in the Venezuelan llanos. *Journal of Wildlife Management*, 67(1), 161-167.

Lloyd- Jones, L. R., Brien, M. L., Feutry, P., Lawrence, E., Beri, P., Booth, S., Coulson, S., Baylis, S. M., Villiers, K., Taplin, L. E. & Westcott, D. A. (2023). Implications of past and present genetic connectivity for management of the saltwater crocodile (*Crocodylus porosus*). *Evolutionary Applications*, 16:911–935.

Lorenz, J. J. (1999). The Response of Physicochemical Changes in the Mangroves of Northern Florida Bay. *Estuaries, 22 (2B)* 500-517.

Luck, N. L., Thomas, K. C., Morin-Adeline, V. E., Barwick, S., Chong, A. Y., Carpenter, E. L. and Medlock, J. 2012. Mitochondrial DNA analyses of the saltwater crocodile (*Crocodylus porosus*) from the Northern Territory of Australia. *Australian Journal of Zoology*, 60(1), 18-25.

Luiselli, L., Akani, G. C., Politano, E. & Odegbune, E. (2006). "Dietary shifts of sympatric freshwater turtles in pristine and altered habitats: The effects of invasive plant species." *Chelonian Conservation and Biology,* 5(1), 25–31.

Lutz, R. S., O'Connor, D. S., & Whelan, A. C. (2015). Spatial ecology and movement patterns of *Crocodylus porosus* in Belize. *Marine Ecology Progress Series*, 533, 243-253.

Machado, A. M., Silva, J. C. R., & Farias, I. P. (2021). Phylogeography and conservation of the black caiman (*Melanosuchus niger*): The largest crocodilian in the Amazon basin. *Conservation Genetics*, 22(1), 1–14.

Magnusson, W. E. (1982). Mortality of eggs of *Caiman crocodilus* crocodilus in central Amazonia, Brazil. *Journal of Herpetology*, 16(2), 121-130.

Magnusson, W. E., & Sanaiotti, T. M. (1995). Growth of *Caiman crocodilus* in central Amazonia: seasonality and its effects on population dynamics. *Journal of Herpetology*, 29(4), 394-396.

Mancina, C. A. & Cruz-Flores, R. (2017). Monitoring programs for biodiversity conservation: A review of key considerations. *Conservation Biology*, *31(4),* 925-935.

Manlik, O., McDonald, J. A., & Alacs, E. A. (2020). Landscape genetics of crocodilian populations: Implications for species management. *Molecular Ecology*, 29(2), 155-170.

Manola, R. & Alcala, A. C. (2015). Conservation of the Philippine crocodile *Crocodylus mindorensis* (Schmidt 1935): in situ and ex situ measures: Philippine crocodile conservation. *Int. Zoo Yb*, 49: 113–124.

Manolis, S. C. (1989). Management of crocodiles in captivity. *Journal of Herpetology*, *23(3):* 143-150.

Margules, C. R. & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, *405(6783)*, 243-253.

Martin, J. E. & Benton, M. J. (2008). Crown clades in vertebrate evolution: The origin of new body plans and their fossil record. *Acta Palaeontologica Polonica*, 53(3), 493-504.

Mascarenhas-Junior, P. G., Correia, J. M. S. & Simoes, P. I. (2023). Tracking crocodylia: a review of telemetry studies on movements and spatial use. *Animal Biotelemetry*, 11(21).

Matanzima, J., Marowa, I., Nhiwatiwa. (2022). Negative human-crocodile interactions in Kariba, Zimbabwe: data to support potential mitigation strategies." *Cambridge University Press.*

Mazaris, A. D., Matsinos, Y. G., & Pantis, J. D. (2005). Evaluating the Impacts of Coastal Erosion on Sea Turtle Nesting. *Ocean & Coastal Management*, *48(1):* 75-88.

Mazzotti, F. J., & Cherkiss, M. S. (2003). Conservation and status of the American crocodile in Florida: Recovering an endangered species while restoring an ecosystem.

Mazzotti, F. J., Best, G. R., Brandt, L. A., Cherkiss, M. S., Jeffery, B. M. and Rice, K. G. (2009). Alligators and Crocodiles as Indicators for Restoration of Everglades Ecosystems. *Ecological Indicators, Vol 9(6),* S137-S149.

Mazzotti, F. J., Brandt, L. A., Moler, P. and Cherkiss, M. S. (2007). American Crocodile (*Crocodylus acutus*) in Florida: Recommendations for Endangered Species Recovery and Ecosystem Restoration. *Journal of Herpetology 41*, 122-132.

Mazzotti, F. J., Jeffery, B. M., & Fujisaki, I. (2019). Population monitoring of *Crocodylus acutus* in Florida. *Estuarine, Coastal and Shelf Science*, 216, 215-225.

Mazzotti, F. J., Jeffery, B. M., Fujisaki, I., & Rice, K. G. (2019). The influence of environmental factors on American alligator (*Alligator mississippiensis*) movement and habitat use. *Herpetological Conservation and Biology*, 14(1), 29-45.

Mazzotti, F. J., Smith, B. J., Squires, M. A., Cherkiss, M. S., Farris, S. C., Hackett, C., Hart, K. M., Gonzales, V. B. and Brandt, L. A. (2019). Influence of Salinity on Relative Density of American Crocodiles (*Crocodylus acatus*) in Everglades National Park: Implications for Restoration of Everglades Ecosystems. *Ecological Indicators: Vol 102*, 608-616.

Mazzotti, F. J.,Best, G. R., Brandt, L. A., Cherkiss, M. S., Jeffery, B. M. & Rice, K. G. (2009). "Alligators and crocodiles as indicators for restoration of Everglades ecosystems." *Ecological Indicators*, 9(6), S137–S149.

McCann, B. E., & Lowe, C. G. (2005). The use of ultrasonic telemetry to study juvenile white shark behaviour. *Environmental Biology of Fishes*, 74(1), 51–61.

McKinnon, E. A., Fraser, K. C., & Stutchbury, B. J. (2013). New discoveries in landbird migration using geolocators, and a flight plan for the future. *The Auk: Ornithological Advances*, 130(2), 211-222.

Medici, E. P. & Desbiez, A. L. J. 2012. Population viability analysis: using a modeling tool to assess the viability of tapir populations in fragmented landscapes. *Integrative Zoology,* 7: 356–372.

Meredith, R. W., Janečka, J. E., Gatesy, J., Ryder, O. A., Fisher, C. A., Teeling, E. C., Goodbla, A., Eizirik, E., Simao, T. L., Stadler, T., Rabosky, D. L., Honeycutt, R. L., Flynn, J. J., Ingram, C. M., Steiner, C., Williams, T. L., Robinson, T. J., Burk-Herrick, A., Westerman, M., ... & Murphy, W. J. (2011). Impacts of the Cretaceous Terrestrial Revolution and KPg extinction on mammal diversification. *Science*, 334(6055), 521–524.

Messel, H., King, F. W., Webb, G. J. W., & Whitaker, R. (1995). *Crocodiles: Status Survey and Conservation Action Plan*. IUCN/SSC Crocodile Specialist Group.

Meyer, A., & Zardoya, R. (1999). Recent advances in the (molecular) phylogeny of vertebrates. *Annual Review of Ecology and Systematics, 30*(1), 564–592.

Miles, L. G., Isberg, S. R., Glenn, T. C., Lance, S. L., Dalzell, P., & Moran, C. (2009). Cross-species amplification of microsatellites in the order Crocodylia. *Conservation Genetics Resources, 1*(1), 3–6.

Milián-García, Y., Venegas-Anaya, M., Ramos-Targarona, R., Rodríguez, S., & Espinosa-López, G. (2020). Conservation genetics of Cuban crocodiles (*Crocodylus rhombifer*) in the wild and captive populations. *Molecular Ecology*, 29(10), 1918-1932.

Milián-García, Y., Venegas-Anaya, M., Ramos-Targarona, R., Rodríguez, S., & Espinosa-López, G. (2020). Conservation genetics of Cuban crocodiles (*Crocodylus rhombifer*) in the wild and captive populations. *Molecular Ecology*, 29(10), 1918-1932.

Mills, L. S. (2007). *Conservation of Wildlife Populations: Demography, Genetics, and Management*. Blackwell Publishing.

Minh, B. Q., Schmidt, H. A., Chernomor, O., Schrempf, D., Woodhams, M. D., Von Haeseler, A., & Lanfear, R. (2020). IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. *Molecular Biology and Evolution*, *37*(5), 1530–1534.

Mitchell, N. J., Allendorf, F. W., Keall, S. N., Daugherty, C. H. & Nelson, N. J. (2008). Demographic effects of temperature-dependent sex determination: will tuatara survive global warming? *Global Change Biology*, *14(6):* 1603-1612.

Morris, W. F. & Doak, D. F. (2002). Quantitative Conservation Biology: Theory and Practice. Sinauer Associates.

Muniz, F., Campos, Z., Rangel, S. H., Martinez, J., Souza, B., Dethoisy, B., Botero-arias, R., Hrbek, T., and Farias, I. 2018. Delimitation of evolutionary units in Cuvier's dwarf caiman, *Paleosuchus palpebrosus* (Cuvier, 1807): Insights from Conservation of a broadly distributed species. *Conservation Genetics*, 19(3):599–610.

Nabholz, B., Glémin, S., & Galtier, N. (2008). Strong variations of mitochondrial mutation rate across mammals—the longevity hypothesis. *Molecular Biology and Evolution, 25*(1), 120–130.

Nadarajan, R., Hassan, R., Gani, M. I., and Hassan, M. A. 2023. Genetic Analysis of Saltwater Crocodile (Crocodylus porosus) from Sarawak River Basin, Sarawak using Cytochrome Oxidase I and Cytochrome b Gene Analysis. *Journal of Survey in Fisheries Sciences,* 10(1) 80-88.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105(49), 19052–19059.

Nei, M. (1987). *Molecular Evolutionary Genetics*. Columbia University Press.

Nei, M., & Kumar, S. (2000). *Molecular Evolution and Phylogenetics*. Oxford University Press.

Norris, D. R. & Marra, P. P. (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor*, *109(3),* 535-547.

Norris, K. (2004). Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigms. *Journal of Applied Ecology, 41(3),* 413-426.

O’Brien, S. J. (1994). A role for molecular genetics in biological conservation. *Proceedings of the National Academy of Sciences*, 91(13), 5748-5755.

Oaks, J. R. (2011). A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. *Evolution*, 65(11), 3285–3297.

Orozco-Terwengel, P., Nagy, Z. T., Vieites, D. R., Vences, M. and Louis JR, E. 2008. Phylogeography and Phylogenetic relationships of Malagasy tree and Ground Boas. *Biological Journal of the Linnean Society*, 2008, 95, 640–652.

Ortega-León, A. M., Morales, A. S., Zamora, G. & Perez-Mendoza, H. (2020). Analysis of the population dynamics of the endangered American crocodile, Crocodylus acutus in Paramillo National Natural Park. *Marine and Freshwater Research* https://doi.org/10.1071/MF19026.

Ortmann-Ajkai, A. (2019). "Traditional ecological knowledge in conservation biology." *Journal of Ethnobiology,* 39(2), 123–135.

Oyler-McCane, K. & Leberg, P. L. (2015). The utility of molecular techniques in wildlife biology: Promises, pitfalls, and progress. *Molecular Ecology*, 24, 3121-3130.

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, 103(929), 91-93.

Panda, A. K., Katdare, S., Gawan, S., Sharma, S. P., Badola, R. & Hussain, S. A. (2023). Population status and factors influencing the distribution of critically endangered gharial (*Gavialis gangeticus*) in a regulated unprotected river system in India. *Global Ecology and Conservation,* 46 (2023) e02547.

Panthum, T., Ariyaraphong, N., Wongloet, W., Wattanadilokchatkun, P., Laopichienpong, N., Rasoarahona, R., Singchat, W., Ahmad, S. F., Kraichak, E., Muangmai, N., Duengkae, P., Fukuda, Y., Banks, S., Temsiripong, Y., Ezaz, T. & Srikulnath, K. (2023). Preserving pure Siamese crocodile populations: A comprehensive approach using multi-genetic tools. *Biology, 12*(11), 1428.

Parker, K. A., et al. (2022). "Reintroduction of wildlife to New Zealand." *Science,* 377(6603), 313–319.

Passos, C., Herrera, E. A., & Barreto, G. R. (2014). Growth patterns in a tropical mammal: Insights from a biphasic model in capybaras (*Hydrochoerus hydrochaeris*). *Acta Theriologica*, 59(1), 27-35.

Peignier, M.-A., Webber, Q. M. R., Koen, E. L., Laforge, M. P., Robitaille, A. L., & Vander Wal, E. (2019). Space use and social association in female caribou: Contrasting the rut and post-rut periods. *Behavioral Ecology, 30*(6), 1697–1708.

Pensoft Publishers. "Genetic study reveals that a captive-bred population could save endangered crocodile from extinction." ScienceDaily. ScienceDaily, 27 July 2023.

Perktaş, U., Elverici, C., & Yaylali, Ö. (2023). Historical demography and climate-driven range shifts in the Blue-spotted Salamander under climate change scenarios. *European Journal of Ecology*, 9(1), 19–30.

Pike, D. A., Webb, J. K., & Shine, R. (2008). Population ecology and conservation of a threatened reptile: the broad-headed snake (*Hoplocephalus bungaroides*). *Biological Conservation, 141(6)*: 1423-1431.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N. & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science, 344(6187)*: 1246752.

Pina, C. I., & Larriera, A. (2001). Growth patterns in *Caiman latirostris* and their relationship with environmental factors. *Journal of Herpetology*, 35(4), 556-560.

Platt, S. G., Rainwater, T. R., & Thorbjarnarson, J. B. (2009). Crocodiles and alligators as indicators for restoration of Everglades ecosystems. *Ecological Indicators*, 9(6), S137–S149.

Pooley, S. (2016). A cultural herpetology of Nile crocodiles in Africa. *Conservation & Society*, 14(4), 391–405.

Pooley, S. (2016). Crocodile conflict in southern Africa: Historical perspectives and current realities. *Oxford Research Encyclopedia of African History*.

Queensland Department of Environment and Science. (2018). *Strategic Plan 2018–2022*.

Rainwater, T. R., Adair, B. M., Platt, S. G., Anderson, T. A., Cobb, G. P. & McMurry, S. T. (2002). Mercury in morelet's crocodile eggs from Belize. *Archives of Environmental Contamination and Toxicology*, 42(3), 319-324.

Rajora, O. P. (2019). Population Genomics: Concepts, Approaches, and Applications. *Springer Nature*.

Ramadani, Afriyanshyah, B. & Hamidy, A. (2023). Population and habitat characteristics of the Saltwater crocodile (*Crocodylus porosus*, Schneider 1801) in the Antan River, Jebus-Parittiga District, West Bangka. *Jurnal Biologi Indonesia*, 19(1): 17-23.

Read, M. A., Georges, A., & Hossack, B. R. (2019). Movement patterns and habitat use of *Crocodylus porosus* in the Australian tropical river systems. *Ecology and Evolution*, 9(12), 7211-7223.

Read, M. A., Grigg, G. C. & Irwin, S. R. (2004). Changes in the distribution of *Crocodylus porosus* in Queensland: 1970-1994. *Biological Conservation*, 70(1), 15-24.

Read, M. A., Grigg, G. C., Irwin, S. R., Shanahan, D., & Franklin, C. E. (2007). Satellite tracking reveals long distance coastal travel and homing by translocated estuarine crocodiles, *Crocodylus porosus*. *PLOS ONE*, 2(9), e949.

Redford, K. H., Adams, W. M. & Mace, G. M. (2011). Synthetic biology and conservation of nature: Wicked problems and wicked solutions. *PLoS Biology*, 9(4), e1001134.

Reed, D. H., Lowe, E. H., Briscoe, D. A., & Frankham, R. (2007). Inbreeding and extinction: The genetic aspects of conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, 38, 135-151.

Reed, J. M., Mills, L. S., Dunning Jr., J. B., Menges, E. S., McKelvey, K. S., Frye, R., Beissinger, S. R., Anstett, M. C. Miller, P. (Year). Emerging issues in population viability analysis. (2021). *Conservation Biology,* Vol 16: 7-19.

Richardson, K. C., Webb, G. J. W. & Manolis, S. C. (2002). *Crocodiles: Inside Out*. Surrey Beatty & Sons.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M. & Schmitz, O. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343(6167), 1241484.

Ritchie, E. G. (2010). Ecology of the dingo (*Canis lupus dingo*) in the Tanami Desert in relation to human–resource subsidies. *Australian Mammalogy,* 32(1), 17–22.

Robitaille, A. L., Webber, Q. M. R., & Vander Wal, E. (2021). The problem and promise of scale in multilayer animal social networks. *Current Zoology, 67*(1), 113–127.

Roche, H., Salas, J., Amaya, D, & Gandini, C. (2009). *Pesticides in American crocodile eggs from Coiba Island National Park, Panama*. Environmental Pollution, 157(1), 87-91.

Rodda, G. H., Fritts, T. H., & Reichel, J. D. (2001). Use of absolute density estimates for monitoring trends in reptile populations: Case study of the brown tree snake on Guam. *Journal of Herpetology, 35(4)*: 589-597.

Rodriguez, J. P., Simonetti, J. A., Premoli, A. C., & Marini, M. A. (2013). Putting conservation priority-setting for marine turtles in context. *Animal Conservation, 14*(1), 1–2.

Rogers, A. R. and Harpending, H. 1996. Population growth makes waves in the distribution of pairwise genetic differences. *Molecular Biology and Evolution, 9*(3), 552–569.

Roman, J., & Palumbi, S. R. (2003). Whales before whaling in the North Atlantic. *Science, 301*(5632), 508–510.

Ross, J. P. (1998). *Crocodiles: Status Survey and Conservation Action Plan*. IUCN/SSC Crocodile Specialist Group.

Ross, J. P. 1998. Crocodiles: An action plan for their Conservation. IUCN/SSC Group Publication. *Croc. Spec*, p. 1-9, 46-47.

Ross, J. P., Abercrombie, C. L., & Thorbjarnarson, J. B. (2020). *Crocodiles: Status Survey and Conservation Action Plan*. IUCN.

Rossi, N. A., Menchaca-Rodriguez, A., Antelo, R., Wilson, B., McLaren, K., Mazzotti, F., & Amato, G. (2020). High levels of population genetic differentiation in the American crocodile (*Crocodylus acutus*). *PLOS ONE*, 15(7), e0235288.

Rozas, J., Ferrer-Mata, A., Sánchez-DelBarrio, J. C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S. E., & Sánchez-Gracia, A. (2017). DnaSP 6: DNA sequence polymorphism analysis of large datasets. *Molecular Biology and Evolution, 34*(12), 3299–3302.

Russello, M. A., Brazaitis, P., Gratten, J., Watkins-Colwell, G. J., and Caccone, A. 2007. Molecular Assessment of the Genetic Integirty, Distinctiveness and Phylogeographic context of the Saltwater Crocodile *(C. porosus)* on Palau. *Conservation Genetics*, 8 (4): 777-787.

Saidman, B. O., Rueda, E. C., Larriera, A., Amavet, P. S. & Vilardi, J. C. (2012). Mating system and population analysis of the broad-snouted caiman (*Caiman latirostris*) using microsatellite markers. *Amphibia-Reptilia, 33*(1), 83–93.

Sajeev, M., Debnath, B., & Ghosh, S. (2019). Genetic diversity and population structure of the Indian mugger crocodile (*Crocodylus palustris*) inferred from mitochondrial DNA sequences. *Mitochondrial DNA Part A*, 30(8), 842–851.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R. & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287(5459),* 1770-1774.

Saldarriaga-Gómez, A. M., Ardila-Robayo, M. C., Medem, F., & Vargas-Ramírez, M. (2023). Hope is the last thing lost: Colombian captive-bred population of the critically endangered Orinoco crocodile (*Crocodylus intermedius*) is a genetic reservoir that could help to save the species from extinction. *Nature Conservation*, 53, 85–103.

Salisbury, S. W. & Willis, P. M. A. (1996). A new crocodyliform from the Early Cretaceous of north-eastern Queensland, Australia. *Memoirs of the Queensland Museum*, 39(2), 343-366.

Sarre, S. D. & Georges, A. (2009). Genetics in wildlife biology: Applications of hypervariable DNA markers in wildlife conservation. *Journal of Conservation Genetics*, 10, 425-438.

Sarre, S. D., & Georges, A. (2009). Genetics in wildlife biology: Applications of hypervariable DNA markers in wildlife conservation. *Journal of Conservation Genetics*, 10, 425-438.

Sawyer, H., Kauffman, M. J., Nielson, R. M., & Horne, J. S. (2009). Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications,* 19(8), 2016–2025.

Schaub, M. & Abadi, F. (2010). Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Animal Ecology*, 80(3), 698-707.

Schenekar, T., & Weiss, S. (2017). Selection and genetic drift in captive versus wild populations: An assessment of neutral and adaptive (MHC-linked) genetic variation in wild and hatchery brown trout (*Salmo trutta*) populations. *Conservation Genetics, 18*(5), 1011–1022.

Schmitz, A., Mansfeld, P., Hekkala, E., Shine, T., Nickel, H., Amato, G. & Böhme, W. (2003). Molecular evidence for species level divergence in African Nile Crocodiles, *Crocodylus niloticus* (Laurenti, 1786). *Evolution*, *2*(8), 703–712.

Scribner, K. T., Lowe, W. H., Landguth, E., Luikart, G., Infante, D. M., Whelan, G. E., & Muhlfeld, C. C. 2016. Applications of Genetic Data to Improve Management and Conservation of River Fishes and Their Habitats. *Fisheries*, 41(4), 174–188.

Seebacher, F., Grigg, G. C., & Beard, L. A. (2003). Crocodiles as dinosaurs: Behavioural thermoregulation in very large ectotherms leads to high and stable body temperatures. *Journal of Experimental Biology*, 206(1), 77-86.

Semeniuk, C., Massalo, A., Hickman, L. and Musiani, M. (2011). Human Activity helps Prey Win the Predator-Prey Space Race. *PLoS ONE, Vol 6 (3)* e17050.

Sergio, F., Newton, I., Marchesi, L., & Pedrini, P. (2008). Ecologically justified charisma: Preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology*, 45(4), 992-1002.

Shannon, G., Dube, M. & Mucklow, S. (2018). Human-wildlife conflict in Africa: From global to local perspectives. *Wildlife Conservation Society Report*.

Shine, R., Somaweera, R., & Webb, G. J. (2019). Empowering local communities in crocodile conservation: The case of Sabah, Malaysia. *Herpetological Review*, 50(4), 670-679.

Simpson, B. K., Bezuijen, M. R., & Behler, J. L. (2006). *Crocodylus porosus* (Schneider, 1801). In S. C. Manolis & C. Stevenson (Eds.), *Crocodiles: Status Survey and Conservation Action Plan* (3rd ed., pp. 99–113). IUCN.

Smith, G. D., Adams, G. L. & Dinkelacker, S. A. (2016). Important habitat characteristics for American Alligators (*Alligator mississippiensis*) on the edge of their range. *Herpetological Conservation and Biology*, 11(1):72–79.

Smith, M. D. (1999). Fishing as a selective process: The role of size-selective harvesting. *Ecology of Fisheries*, 21(4), 458-468.

Sodhi, N. S., Posa, M. R. C., Lee, T. M., Bickford, D., Koh, L. P. & Brook, B. W. (2010). The state and conservation of Southeast Asian biodiversity. *Biodiversity and Conservation*, 19(2), 317-328.

Somaweera, R., Shine, R. & Webb, J. K. (2013). Human-crocodile conflict in the context of wildlife conservation. *Wildlife Research*, *40(4):* 280-287.

Somaweera, R., Shine, R., & Webb, J. K. (2018). The influence of human activity on the genetic structure of crocodilian populations: Implications for conservation. *Conservation Genetics*, 19(3), 485-499.

Spoelman, R. J., Terpstra, J. W., & Pennings, H. J. (2004). Low genetic variation and its relation to population extinction risks. *Conservation Biology*, 18(3), 75-83.

Stevenson, C. & Whitaker, R. (2010). Crocodilian conservation in South Asia. *Herpetological Review*, 41(2), 140-145.

Stuebing, R. B. & Shahrul, A. M. S. (1992). Population Characteristics of the Indo-Pacific Crocodile (*Crocodylus porosus* Schneider) in the Klias River, Sabah. Paper presented at the 1lth Working Meeting of the IUCN-SSC, Crocodile Specialist Group, Victoria Falls, Zimbabwe.

Stuebing, R. B., Bezuijen, M. R., Auliya, M., & Voris, H. K. (2014). Conservation and management of the saltwater crocodile (*Crocodylus porosus*) in Sabah, Malaysia. *Tropical Conservation Science*, 7(3), 453-465.

Stuebing, R. B., Ismail, G. and Ling, H. C. (1994). The Distribution and Abundance of the Indo-pacific Crocodile *Crocodylus porosus* Schneider in the Klias River, Sabah, East Malaysia. *Biological Conservation, 69 (1)*, 1-7.

Stuebing, R. B., Sompud, J., & Ismail, M. G. (2002). The status of crocodiles in the Kinabatangan River, Sabah, Malaysia: Results of a survey and management recommendations. Sabah Wildlife Department Research Bulletin, 5, 12-18.

Sukumar, R., & Sinha, A. (2018). The impact of hydroelectric dams on the population dynamics of Siamese crocodiles (*Crocodylus siamensis*) in Cambodia. *Conservation Biology,* 32(3), 688-698.

Tajima, F. (1989). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics, 123*(3), 585–595.

Tamura, K., Stecher, G. and Kumar, S. 2021. MEGA11: Molecular Genetics Analysis version 11. *Molecular Biology and Evolution* 38:3022-3027.

Tamura, K., Stecher, G., and Kumar, S., 2021. MEGA11: Molecular Evolutionary Genetics Analysis Vs.11. *Molecular Biology and Evolution*, Volume 38, Issue 7, July 2021, Pages 3022–3027.

Taplin, L. E. & Grigg, G. C. (1989). Historical perspectives of crocodilian osmoregulation and the relevance to archosaurian physiology. *American Zoologist*, 29(3), 983-1001.

Taylor, D., Abernethy, K. & Taplin, L. (2017). Impacts of pollutants on crocodilian populations. *Environmental Science and Pollution Research*, *24(10):* 8974-8985.

Templeton, A. R., Routman, E., & Phillips, C. A. (1992). Separating population structure from population history: A cladistic analysis of the geographical distribution of mitochondrial DNA haplotypes in the tiger salamander, *Ambystoma tigrinum*. *Genetics, 132*(4), 619–633.

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., Lambert, T. D., & Balbas, L. (2001). Ecological meltdown in predator-free forest fragments. *Science,* 294(5548), 1923–1926.

Than, K. Z., Strine, C. T., Sritongchuay, T., Zaw, Z. and Hughes, A. C. (2020). Estimating Population Status and Sire Occupancy of Saltwater Crocodiles *Crocosylus porosus* in the Ayeyarwady Delta, Myanmar: Inferences from Spatial Modeling Techniques. *Global Ecology and Conservation 24 (2020)* e01206.

The Borneo Post. (2022, September 18). Possible reasons behind crocodile-human conflict in Sabah. Retrieved from https://www.theborneopost.com

The Borneo Post. (2024). Crocodile attack in Sarawak. Retrieved from https://www.theborneopost.com

The Star. (2024, June 24). Sabah Wildlife Dept hard-pressed to cope with increasing human-croc conflict. Retrieved from https://www.thestar.com.my

The Vibes. (2023, January 15). Rise in Sabah crocodile attacks caused by depleting food source: Conservationist. Retrieved from https://www.thevibes.com

Thorbjarnarson, J. (1992). Crocodiles: An action plan for their conservation. *IUCN Species Survival Commission*.

Thorbjarnarson, J. (1996). Reproductive characteristics of the order Crocodylia. *Herpetologica*, 52(1), 8-24.

Thorbjarnarson, J. (1999). Crocodilian conservation and management. *In Crocodiles: Status Survey and Conservation Action Plan* (pp. 3-13). IUCN Crocodile Specialist Group.

Thorbjarnarson, J. (1999). Ecology of the American crocodile, *Crocodylus acutus*. *Journal of Herpetology*, 33(3), 366-374.

Thorbjarnarson, J. B. (1992). Crocodiles: An action plan for their conservation. *IUCN-The World Conservation Union*.

Thorbjarnarson, J. B., Platt, S. G. & Lee, K. (2006). "Crocodile conservation and management in Southeast Asia." *Crocodile Specialist Group Newsletter, 25(2):* 4-9.

Treves, A., Wallace, R. B., Naughton-Treves, L. & Morales, A. (2006). Co-managing human-wildlife conflicts: A review. *Human Dimensions of Wildlife*, 11(6), 383-396.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C. & Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359(6374), 466-469.

Tucker, M. A., Ord, T. J. & Rogers, T. L. (2005). The role of temporal and spatial factors in the regulation of animal populations. *Ecological Monographs*, *75(4),* 523-544.

Unajak, S., Meesawat, P., Anyamaneeratch, K., Anuwareepong, D., Suthithaworn, P., & Na-Nakorn, U. (2017). Genetic diversity of captive *Crocodylus porosus* populations in Thailand and implications for future conservation programs. *PLOS ONE, 12*(9), e0184526.

Van Asch, B., Versfeld, W. F., Hull, K. L., Leslie, A. J., Matheus, T. I., Beytell, P. C., du Preez, P., Slabbert, R., & Rhode, C. (2019). Phylogeography, genetic diversity, and population structure of Nile crocodile populations at the fringes of the southern African distribution. *PLOS ONE*, 14(12), e0226505.

Van Weerd, M., & van der Ploeg, J. (2012). The Philippine crocodile: Ecology, culture, and conservation. *Herpetological Review*, 43(1), 70-79.

Veach, V., Moilanen, A., & Di Minin, E. (2017). Threats from urban expansion, agricultural transformation and forest loss on global conservation priority areas. *PLOS ONE,* 12(11).

Venegas-Anaya, M., Balaguera-Reina, S., & Lessios, H. A. (2015). Reproductive ecology and hatchling growth rates of the American crocodile (*Crocodylus acutus*) on Coiba Island, Panama. *Journal of Natural History*, *44(7)*: 741-761.

Venegas-Anaya, M., Crawford, A. J., Escobedo-Galván, A. H., Sanjur, O. I., Densmore III, L. D., & Bermingham, E. (2008). Mitochondrial DNA phylogeography of *Caiman crocodilus* in Mesoamerica and South America. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, 309A(10), 614–627.

Versfeld, W. F. 2016. Nile Crocodile (Crocodylus niloticus) Genetic Diversity and Population Structure within the Lower Kunene and Okavango Rivers of Northern Namibia. *Msc Thesis, Stellenbosch University.*

Vila, C., Amorim, I. R., Leonard, J. A., Posada, D., Castroviejo, J., Petrucci-Fonseca, F., Crandall, K. A., Ellegren, H., & Wayne, R. K. (1999). Mitochondrial DNA phylogeography and population history of the grey wolf (*Canis lupus*). *Molecular Ecology, 8*(12), 2089–2103.

Vitt, L. J. & Caldwell, J. P. (2014). Herpetology: An Introductory Biology of Amphibians and Reptiles. 4th Edition. Academic Press. Pp 776.

Wallace, K., Leslie, A. J., Coulson, T. and Wallace, A. S., (2013). Population Size and Structure of the Nile Crocodile *Crocodylus niloticus* in the Lower Zambezi Valley. *Oryx, 47 (3),* 457-465.

Walsh, B. & Whitehead, P. J. (1993). Problem Crocodiles, *Crocodylos porosus*, at Nhulunbuy, Northern Territory: An Assessment of Relocation as a Management Strategy. *Wildlife Research: 20 (1)* 127-135.

Walsh, B., & Whitehead, P. J. (1993). Problem crocodiles, *Crocodylus porosus*, at Nhulunbuy, Northern Territory: An assessment of relocation as a management strategy. *Wildlife Research*, 20(1), 127–135. https://doi.org/10.1071/WR9930127

Weaver, J. P., Rodriguez, D., Venegas-Anaya, M., Cedeño-Vázquez, J. R., Forstner, M. R. J., and Densmore, L. D. 2008. Genetic characterization of captive Cuban crocodiles (*Crocodylus rhombifer*) and evidence of hybridization with the American crocodile (*Crocodylus acutus*). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, 309A (10), 649–660.

Webb, G. J. W. & Manolis, C. 1989. Crocodile conservation in northern Australia. *Biological Conservation*, 48(3), 243-253.

Webb, G. J. W. & Manolis, S. C. (1989). Crocodile management and population dynamics: Lessons from Australia. *Surrey Beatty & Sons Pty Ltd*.

Webb, G. J. W. & Manolis, S. C. (1989). *Crocodiles of Australia*. Reed Books.

Webb, G. J. W. & Manolis, S. C. (2010). *Crocodile management and conservation in Australia: 30 years of success*. CSIRO Publishing.

Webb, G. J. W. and Smith, A. M. A. (1984). Sex Ratio and Survivorship in the Australian Freshwater Crocodile, *Crocodylus johnstoni*. The Structure, Development and Evolution of Reptiles, ed. by M.W.J. Ferguson. Academic Press: London. Pp. 319-355.

Webb, G. J. W., & Smith, A. (1987). Crocodile population dynamics and management strategies. *Journal of Herpetology, 23*: 7-21.

Webb, G. J. W., Manolis, S. C. & Brien, M. L. (2010). Conservation and management of the saltwater crocodile (*Crocodylus porosus*) in Northern Australia: 1971–2007. *Wildlife Research*, *37(8),* 691-702.

Webb, G. J. W., Manolis, S. C. & Brien, M. L. (2021). Human-crocodile conflict in Northern Australia: Lessons from 40 years of successful management. *Wildlife Research*, 48(4), 325-338.

Webb, G. J. W., Manolis, S. C., & Brien, M. L. (2010). Conservation and management of the saltwater crocodile (*Crocodylus porosus*) in Northern Australia: 1971–2007. *Wildlife Research*, 37(8), 691-702.

Webb, G. J. W., Manolis, S. C., & Brien, M. L. (2010). Saltwater crocodile *Crocodylus porosus*. In S. C. Manolis & C. Stevenson (Eds.), *Crocodiles: Status Survey and Conservation Action Plan* (pp. 99-113). IUCN Crocodile Specialist Group.

Webb, G. J. W., Manolis, S. C., & Brien, M. L. (2018). Crocodile management in the Northern Territory of Australia: A successful, sustainable use program. *Journal of Wildlife Management*, 82(2), 317-327.

Webb, G. J. W., Manolis, S. C., & Buckworth, R. (1978). Crocodylus porosus and Crocodylus johnsoni: growth, demography, and conservation. *Wildlife Research*, 5(3), 385-395.

Webb, G. J. W., Messel, H., & Magnusson, W. (1977). The nesting biology of Crocodylus porosus: Clutch size, nest distribution and nest success at a major nesting site in northern Australia. *Wildlife Research*, 4(4), 529-540.

Webb, G. J. W., Sack, G. C., Buckworth, R. and Manolis, S. C. (1983). An Examination of *Crocodylus porosus* Nests in two Northern Australian Freshwater Swamps, with an Analysis of Embryo Mortality. *Aust. Wildlife. Res. 10*: 571-605.

Webb, G. J. W., Sack, G. C., Buckworth, R., & Manolis, S. C. (1983). Crocodylus porosus population dynamics and nest ecology in Northern Australia. *Journal of Herpetology*, *17(3):* 141-146.

Whitaker, R. & Whitaker, N. (2008). Who's got the biggest? *Crocodile Specialist Group Newsletter*, 27(4), 26-30.

Whitaker, R. (1984). Preliminary Survey of Crocodiles in Sabah, East Malaysia. *WWF Report*, 1-71.

Whitaker, R., & Basu, D. (1983). The crocodilian resources of India and the development of crocodile farming. *Journal of the Bombay Natural History Society, 79*(3), 531–548.

Wiens, J. J. (1998). Combining data sets with different phylogenetic histories. *Systematic Biology, 47*(4), 568-581.

Wijesundara, A. A. S. G. & Karawita, K. V. D. H. R. (2024). Human-crocodile conflict in sri lanka: threats and habitat vulnerability analysis. Proceedings of 13th Annual Science Research Session 2024, FAS, SEUSL, 6th November 2024.

Wilcove, D. S., Giam, X., Edwards, D. P., Fisher, B. & Koh, L. P. (2013). Navjot's nightmare revisited: Logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution*, 28(9), 531-540.

Wildlife Conservation Action. (n.d.). *Progress in the fight against human-wildlife conflicts: Lessons from Mola Ward 3*.
Retrieved from https://www.wildlifeconservationaction.org/post/progress-in-the-fight-against-human-wildlife-conflicts.

Willi, Y. & Hoffmann, A. A. 2009. Genetic rescue can prevent extinction of small populations from inbreeding depression. *Nature*, 463(7277), 347-349.

Woodward, A. R., Rice, K. G. & Percival, H. F. (2010). Crocodilian habitat suitability and population status. *Wetlands Ecology and Management*, 18(3), 229-240.

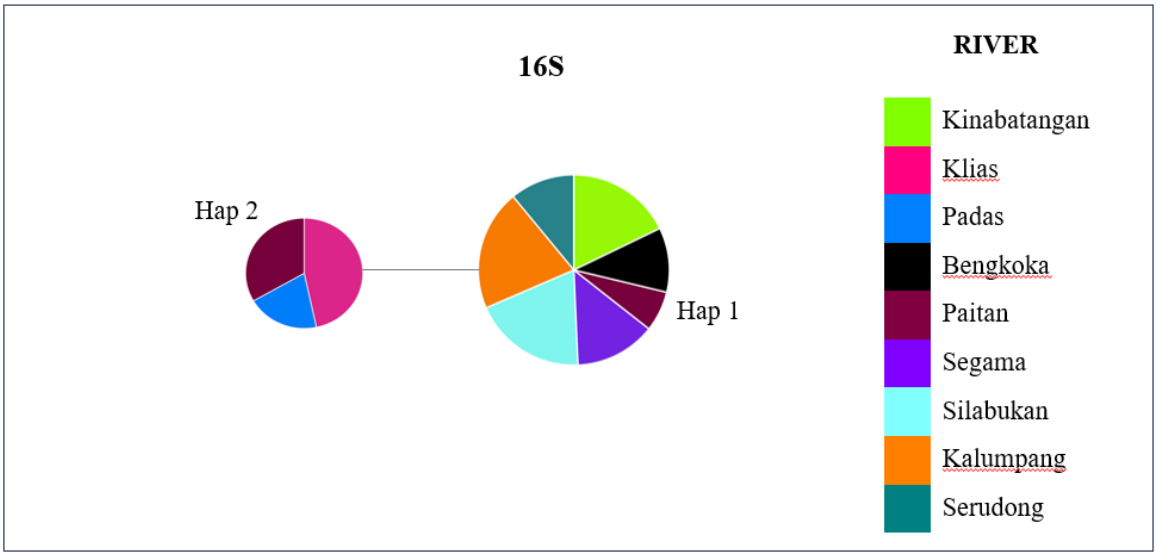
Woodward, A. R., Rice, K. G., & Linda, S. B. (1995). Survivorship of juvenile alligators in north-central Florida. *Journal of Herpetology, 29(3):* 507-513.

Wright, S. (1931). Evolution in Mendelian populations. *Genetics, 16*(2), 97–159.

Wu, X. B., Ding, Y. Z., Liu, N. F., Zhang, Y. P. & Wu, G. (2002). Conservation of Chinese alligator (*Alligator sinensis*): What has been done and what should be done. *Biodiversity & Conservation*, 11(8), 1647-1659.

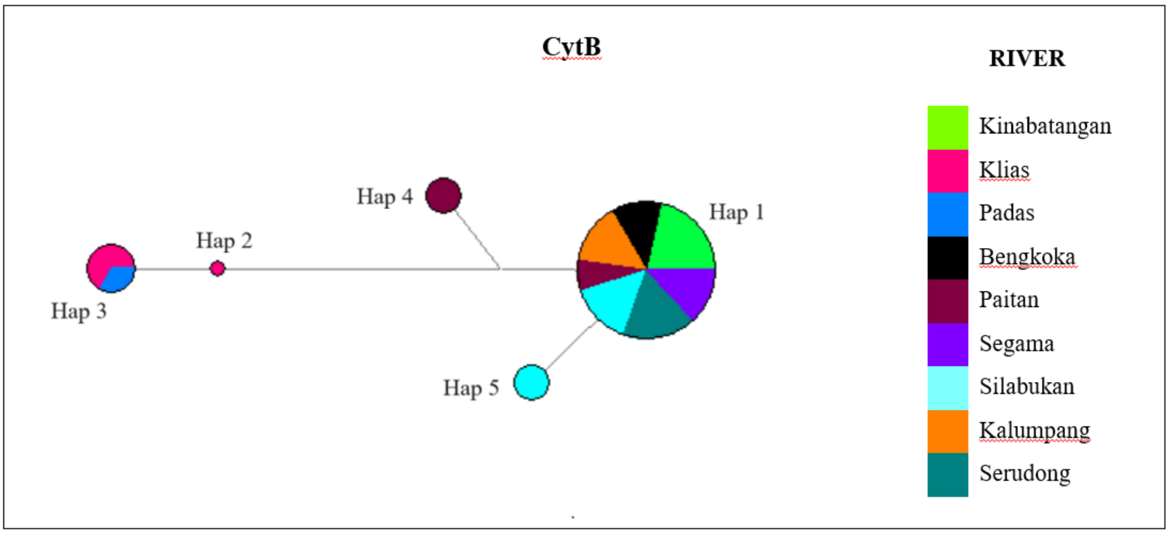
Yussop, Y. (2024, October 23). SFC records five croc attacks in Bintulu between 2020–2024, three fatal. *Borneo Post Online*. Retrieved from https://www.theborneopost.com

APPENDIX I Neighbour joining haplotype network of *C. porosus* 16S region



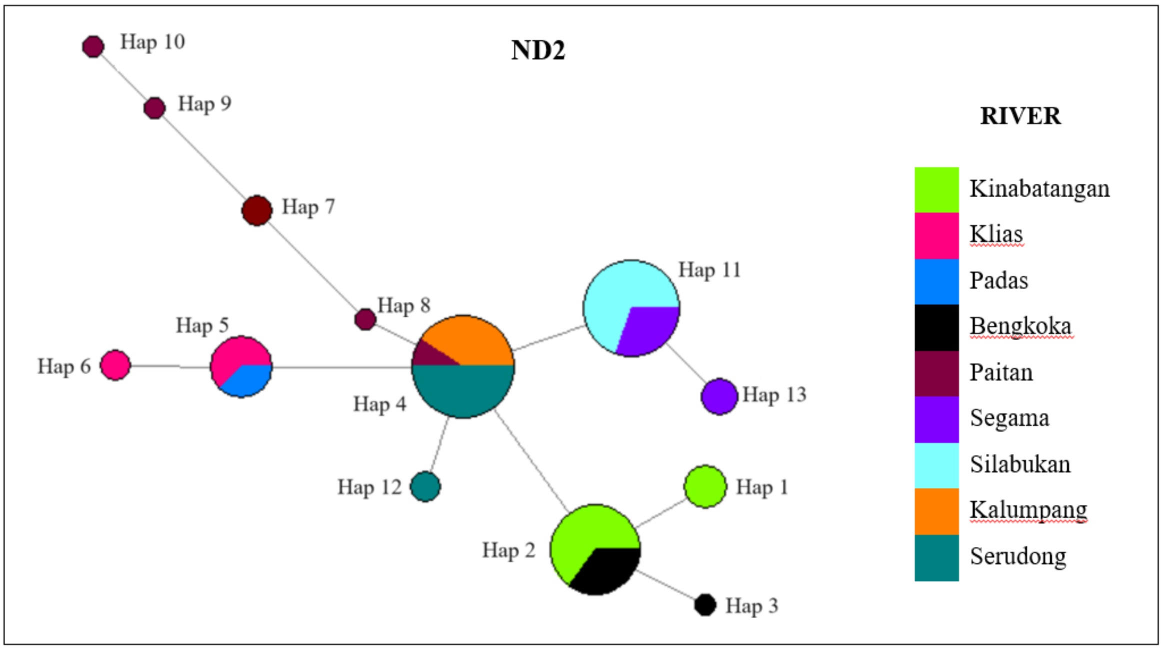
Neighbour joining haplotype network of *C. porosus* 16S region. Area of each circle is proportional to haplotype frequency.

APPENDIX II Neighbour joining haplotype network of *C. porosus* CytB region



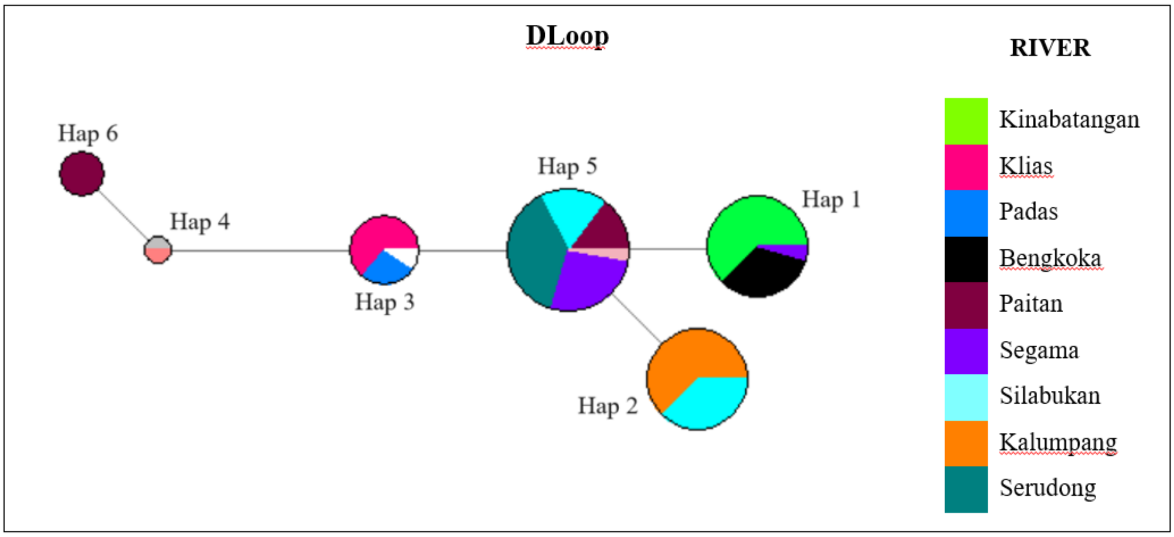
Neighbour joining haplotype network of *C. porosus* CytB region. Area of each circle is proportional to haplotype frequency.

APPENDIX III Neighbour joining haplotype network of *C. porosus* ND2 region



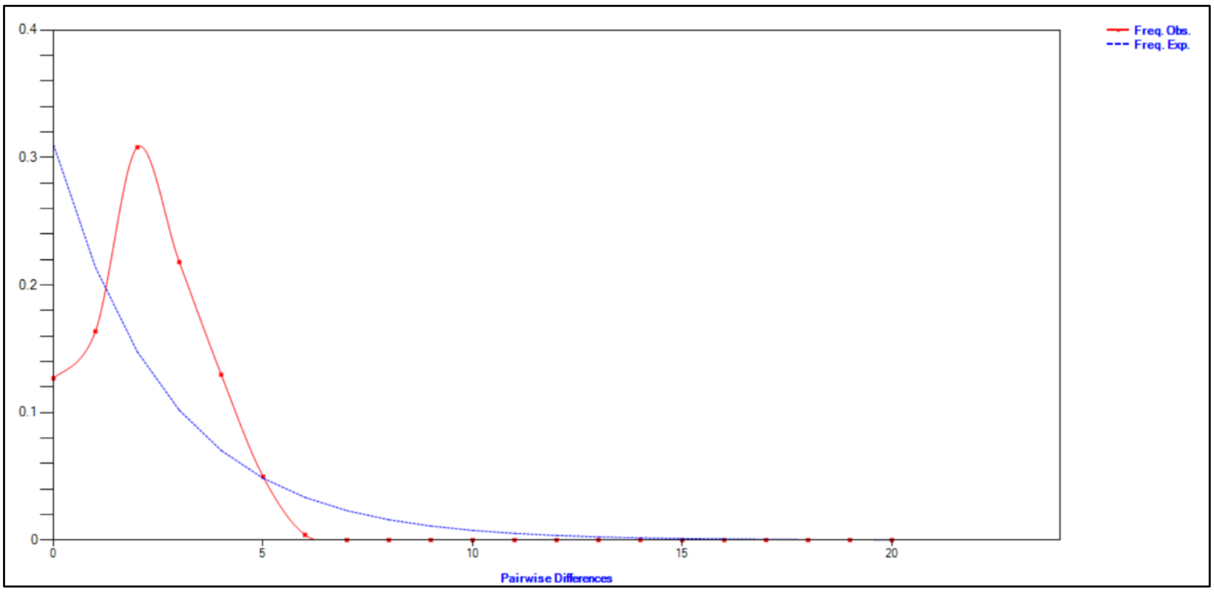
Neighbour joining haplotype network of *C. porosus* ND2 region. Area of each circle is proportional to haplotype frequency.

APPENDIX IV Neighbour joining haplotype network of *C. porosus* D-loop region



Neighbour joining haplotype network of *C. porosus* D-Loop region. Area of each circle is proportional to haplotype frequency.

APPENDIX V Mismatch distribution for the East Coast population excluding Paitan River.



Mismatch distribution graph of *C. porosus* East Coast populations without Paitan River. Axis-x: pairwise differences, Axis-y: frequency of pairwise comparisons, green dotted line: expected frequency under a hypothesis of population expansion, red line: frequency observed.