

# Direct and indirect interactions with vegetation shape crocodylian ecology at multiple scales

Ruchira Somaweera<sup>1,2</sup>  | Mathew L. Brien<sup>3</sup> | Steven G. Platt<sup>4</sup> | Charlie Manolis<sup>5</sup> | Bruce L. Webber<sup>1,2,6</sup>

<sup>1</sup>CSIRO Land and Water, Floreat, Western Australia, Australia

<sup>2</sup>School of Biological Sciences, University of Western Australia, Crawley, Western Australia, Australia

<sup>3</sup>Queensland Parks and Wildlife, Bentley Park, Queensland, Australia

<sup>4</sup>Wildlife Conservation Society, Bronx, New York, USA

<sup>5</sup>Wildlife Management International Pty. Limited, Karama, Northern Territory, Australia

<sup>6</sup>Western Australian Biodiversity Science Institute, Perth, Western Australia, Australia

## Correspondence

Ruchira Somaweera, CSIRO Land and Water, Floreat, Western Australia, Australia.  
Email: ruchira.somaweera@csiro.au

## Funding information

Australian Government's National Environment Science Program

## Abstract

1. As one of the world's largest predators of freshwater environments, crocodylians play an important role in shaping their community. In turn, many aspects of crocodylian life histories are influenced and have been shaped by characteristics of their environment, especially vegetation. However, our understanding of just how vegetation impacts crocodylian life histories remains limited, particularly in regard to indirect interactions. Such interactions can be critical for understanding population dynamics and, therefore, for informing conservation management decisions.
2. We reviewed contemporary understanding of these plant–crocodylian interactions in peer-reviewed journals and the *grey literature*, synthesising life history-shaping dynamics against aspects of their ecology. We then conceptualised how global environmental change, including climate change, species invasions and land use change, may threaten these critical dependencies, and how future conservation plans need to account for these pressures.
3. We identified five primary aspects of crocodylian ecology—habitat selection, nesting ecology, communication, physiology, and feeding ecology—that are probably shaped by vegetation interactions at different spatial scales. These interactions include direct and indirect impacts, with both positive and negative outcomes from a crocodylian perspective.
4. Anthropogenic impacts on environments via global environmental change drivers is causing unprecedented change to vegetation dynamics. What is often overlooked is how these changes impact large aquatic predators such as crocodylians. Our synthesis shows that while many impacts can be identified, their magnitude and mechanism are not well understood, making management driven mitigation challenging. We recommend that future studies prioritise quantifying how vegetation communities shape the suitability of crocodylian nest sites, and how to best detect the fingerprint of impacts caused by invasive alien plants on demographic change in crocodylians over longer durations. An improved understanding of the impact of vegetation impacts on crocodylians is essential for building effective conceptual frameworks and management agendas for the conservation of these iconic reptiles.

## KEYWORDS

alligator, crocodile, global environmental change impacts, life history, plant–animal interactions

## 1 | CROCODYLIANS IN A CHANGING WORLD

Crocodylians are an ancient and highly successful lineage of reptiles that have retained their basic body form and function for almost 250 million years (Brazaitis & Watanabe, 2011; Seymour, Bennett-Stamper, Johnston, Carrier, & Grigg, 2004). These survivors have demonstrated a high degree of adaptability and resilience to past, present, and likely future environmental change. Crocodylians are also near-exclusively carnivorous and occupy the top position in most tropical and subtropical aquatic food webs. Relative to terrestrial or marine environments, this places them in equivalent positions to the large dominant carnivores regularly referred to as apex predators or keystone species (Wallach, Izhaki, Toms, Ripple, & Shanas, 2015).

Crocodylians are considered the most economically valuable of all the reptiles, with global industries in skin, meat, tourism and trophy hunting worth many millions of dollars annually (Caldwell, 2017; Webb, 2014). Economically driven sustainable-use programmes have underpinned many of the successful conservation programs since the 1980s. These programmes have been critical to the survival of many crocodylian species that can otherwise pose a serious threat to humans and their livelihoods (Ross, 1995; Thorbjarnarson, 1999). Beyond pure economic values, crocodylians also have social value from a cultural perspective. That is, crocodylians have aesthetic, recreational, spiritual, and psychological values in many cultures and indigenous value systems around the world (Olupona, 1993; Passariello, 1999; Skinner, 1964).

However, despite having high economic and cultural value and a reputation for having “held their own with the dinosaurs,” increasingly efficient human hunting pressure has led to significant declines in crocodylian numbers around the world. Conservation efforts in recent decades, and an end to widespread and uncontrolled hunting, have reversed downward population size trends in some countries (Fukuda et al., 2011; Mazzotti, Brandt, Moler, & Cherkiss, 2007; Mazzotti, Cherkiss, Parry, & Rice, 2007). In less developed countries, however, population declines continue due to deliberate and accidental killings, habitat modification, and urbanisation (Ashton, 2010; Platt & Thorbjarnarson, 2000; Thorbjarnarson & Hernández, 1992). These declines often happen despite legislation that prohibits the primary cause.

Policy-based protection alone is highly ineffective for the conservation of species if suitable habitat and ecological requirements for population viability are not maintained. Robust conservation management depends also on a solid understanding of the life history of the species in question. As most crocodylian behaviours are cryptic in nature, many aspects of their ecology remain unknown or poorly documented for more than half of the 25 extant species (Ross, 1998; Somaweera, Brien, & Shine, 2013). An increased understanding of their ecological needs, including niche characterisation, environmental requirements, and ecophysiological tolerances/preferences, is essential for building effective conceptual frameworks to prioritise conservation management agendas.

As a group of large aquatic predators, crocodylians play an important role in the coastal and wetland environments that they inhabit, due to their large biomass and ability to feed at various trophic levels (Nifong, 2018). In turn, crocodylian life histories have been shaped from an evolutionary perspective by the surrounding environment. For example, movement patterns and habitat use (Kofron, 1992), reproduction (Magnusson, Lima, & Sampaio, 1984), feeding and predation (Somaweera, Webb, & Shine, 2011), genetic flow (Dever, Strauss, Rainwater, McMurry, & Densmore Iii, 2002), and social interactions (Lang, 1987) are influenced by environment characteristics. However, it is still largely unknown how the vegetative elements of their environment shape crocodylian life histories, relative to other biotic and abiotic components such as microclimate, local geology and other co-occurring fauna.

Here, we provide a synthesis of how crocodylian life histories are shaped and influenced by the vegetative components of their surrounding environment. Where possible, we aim to identify process as well as pattern behind the insight provided. We partition these plant-animal interactions across different aspects of their ecology and between direct and indirect impacts, both positive and negative. Finally, we summarise how global environmental change, including climate change, species invasions and land use change, may threaten these plant-animal interactions and how future conservation efforts need to account for these increasing additional pressures.

To this end, we examined peer-reviewed journals, the *grey literature*, and accounts from experienced ecologists on the relationship between crocodylian life histories and vegetation. Including the grey literature (those published in scientific and technical reports, field guides, and newsletters) as well as accounts from the authors and colleagues were particularly important in our investigation, given the paucity of peer-reviewed sources on this topic. Such records typically comprise anecdotal observations, often based upon small sample sizes, but merit inclusion as long as they exhibit adequate levels of methodological rigor similar to published literature and their interpretation is not overstated (Conn, Valentine, Cooper, & Rantz, 2003). Collections of these anecdotes can suggest trends (Safina, 2015), and by ignoring such reports, we would overlook a rich source of field observations (Bates & Byrne, 2007; Simkhada, Knight, Reid, Wyness, & Mandava, 2005).

## 2 | VEGETATION INTERACTIONS AND OUTCOMES

Many critical aspects of crocodylian ecology are influenced by vegetation at a range of spatial scales, via both direct and indirect pathways. We discuss these interactions and influences under five separate life history parameters: habitat ecology, nesting ecology, communication, physiology, and foraging and feeding ecology.

## 2.1 | Habitat ecology

It is widely accepted that crocodylians are habitat generalists, with no strong affiliation for any specific type of landscape-level vegetation community as their core place of occupancy (Grigg & Kirshner, 2015). For example, American alligators (*Alligator mississippiensis*) occupy coastal habitats (brackish marshes, intermediate marshes, freshwater marshes, coastal lakes and even saltwater marshes) as well as inland areas (marshes, bayous, swamps, natural lakes, reservoirs, lakes, creeks, and ditches), each with contrasting vegetation communities (as reviewed by Staton, 1989; Wilkinson, 1984). In Sri Lanka, the mugger crocodile (*Crocodylus palustris*) occupies a wide range of both natural and anthropogenic inland aquatic habitats, including paddy field canals, agro-wells, rivers, streams, irrigation canals, man-made lakes, swamps, and even water-filled excavations (De Silva, 2013;

R. Somaweera personal observation). In northern tropical Australia, freshwater crocodiles (*Crocodylus johnstoni*) inhabit all freshwater environments including minor and often ephemeral headwaters, and the downstream broad tidal reaches of major rivers (Webb, Manolis, & Sack, 1983). The riparian margins and underwater vegetation of these environments range from sparsely to highly vegetated and from simple to complex in structure, and they occur across a wide range of climatic and floristic zones. Crocodylians also readily adapt to anthropogenically modified environments with substantially different vegetation composition relative to natural environments (e.g. American crocodile [*Crocodylus acutus*] in spoil banks [Kushlan & Mazzotti, 1989a]; Chinese alligator [*Alligator sinensis*] in agricultural ponds [Thorbjarnarson, Wang, & He, 2001]). It is reasonable to assume, therefore, that at a landscape-level site selection by crocodylians is essentially independent of specific vegetation communities.



**FIGURE 1** Direct and indirect interactions between crocodylians and vegetation. (a) A female Australian freshwater crocodile (*Crocodylus johnstoni*) guarding her crèche among littoral aquatic vegetation in Australia (Photo: R. Somaweera). (b) A mugger crocodile (*Crocodylus palustris*) basking on a fallen tree in a marsh overgrown by water hyacinth (*Eichhornia crassipes*) and other weeds in Sri Lanka (R. Somaweera). (c) An American alligator (*Alligator mississippiensis*) nest constructed using grasses (P. Trosclair/R. Elsey). (d) A female saltwater crocodile (*Crocodylus porosus*) nesting among palm fronds in captivity in Malaysia (R. Somaweera). (e) The invasive weed stinking passionflower (*Passiflora foetida*) smothering the nesting habitat of *C. johnstoni* in north-west Australia (R. Somaweera). (f) A Philippine crocodile (*Crocodylus mindorensis*) basks in a tree at a non-tidal water body in the Philippines (M. van Welsem/Mabuwaya Foundation). (g) Two juvenile broad-nosed caimans (*Caiman latirostris*) feeding on fruits of *Philodendron selloum* in captivity in south-eastern Brazil (D. V. Andrade). (h) An *A. mississippiensis* with likely incidental placement of water plants on its back (S. Foote)

### 2.1.1 | Spatial distribution and survivorship

At a more local site level, vegetation can affect certain aspects of habitat ecology across all life stages. For example, the density and structure of vegetation (littoral, aquatic) is a critical element for determining ontogenetic niche partitioning across all age groups. In general, crocodylians prefer environments characterised by calm, sheltered, permanent water bodies with low salinity and littoral and aquatic vegetation that serve as both cover for individuals and as a refuge for prey (Cott, 1961; Ouboter & Nanhoe, 1988; Villegas & Reynoso, 2013). In stable populations, adults and sub-adults are often found in the more open parts of waterbodies, with hatchlings and juveniles occupying the heavily vegetated edges and smaller waterways, which protect against predation (both from larger conspecifics as well as other predators: Somaweera et al., 2013). Heavily vegetated habitat also minimises exposure to thermal extremes and wave action (Kushlan & Mazzotti, 1989b) while providing a refuge for potential prey (e.g. insects, frogs; Temsiripong, 1999).

Preference for vegetated sites over non-vegetated sites by hatchling and juvenile crocodylians has been demonstrated for several crocodylians including the common caiman (*Caiman crocodylus*; Glastra, 1983), black caiman (*Melanosuchus niger*; Da Silveira, Magnusson, & Campos, 1997), *A. mississippiensis* (Smith, Adams, & Dinkelacker, 2016), Nile crocodile (*Crocodylus niloticus*; Honegger, 1971), Morelet's crocodile (*Crocodylus moreletii*; Cedeño-Vázquez, Ross, & Calmé, 2006), and *C. johnstoni* (Somaweera et al., 2011; Figure 1a), with lower rates of survivorship in environments with little to no vegetation cover due to higher predation (Rootes & Chabreck, 1993).

Hatchling survivorship has also been negatively correlated with distance between nest sites and suitable nursery habitat, the latter of which is characterised by reasonably dense vegetation cover (Mazzotti, 1999; Mazzotti, Cherkiss, Parry & Rice, 2007). Seasonal fluctuations in floodwaters can also provide either an increase or decrease in available vegetative cover depending on the adjacent habitat (Honegger, 1971). In lotic waters, where floating vegetation is scarce, underwater exposed root systems and fallen trees may be used as nursery habitat (Steel, 1989).

In contrast, the proliferation of invasive and introduced aquatic plants in lake environments often reduces the amount of open water areas and hinders movement and navigation of crocodiles, especially larger individuals (Rajbhandari & Acharya, 2014; Figure 1b). For example, in Uganda, very few large (>2 m) *C. niloticus* were observed in waters choked with the invasive alien weed *Pistia stratiotes* (Parker, 1970). While anecdotal reports suggest that this can lead to decreased densities over time for crocodylians, the confounding effect of reduced detectability due to thicker vegetation makes it difficult to validate such trends if they are based on opportunistic surveys alone.

The construction of dens by some species of crocodylian serves as overwintering and aestivation sites (Platt, 2000; Thorbjarnarson & Wang, 2010). The location of these dens often depends on the

presence of bank vegetation, such as tree roots, which provide structural support. An association of dens and tree roots, especially fibrous root mats suspended in the water, has been reported for *A. mississippiensis* (Kushlan, 1974), *C. acutus* (Thorbjarnarson, 1989), *C. johnstoni* (Walsh, 1989), *C. moreletii* (Álvarez Del Toro, 1974; Platt, 2000), *C. palustris* (Deraniyagala, 1939; Whitaker & Whitaker, 1984), and the Siamese crocodile (*Crocodylus siamensis*; Simpson, 2006). Deraniyagala (1939) further reported that *C. palustris* favours Arjun tree (*Terminalia arjuna*) root systems as resting places, as they provide ideal hiding places. Therefore, it is likely that vegetation plays a crucial role in determining the spatial occupancy and therefore the survivorship of crocodylians within a habitat.

By contrast, adult crocodylians can also indirectly impact the localised composition and richness of plant species owing to their large size. In the Florida Everglades, alligators create disturbance patches known as *gator holes*. The creation and maintenance of these holes by alligators influences plant community composition and structure and increases the richness of vascular plants in and around the holes relative to the surrounding marsh (Palmer & Mazzotti, 2004). Therefore, the synergies between crocodylians and vegetation are often self-reinforcing.

## 2.2 | Nesting ecology

### 2.2.1 | Nest site selection

In oviparous animals such as crocodylians, the condition and availability of suitable nest sites have critical consequences for the lifetime fitness of progeny as well as the overall demographics of the population. As reviewed in Refsnider (2016), nest site selection in reptiles is driven by multiple evolutionary factors, but it is widely accepted that the factors governing nest site selection are one of the most poorly understood aspects of crocodylian behaviour (Lang, 1987). Nest site selection represents an optimisation process balancing (1) optimal conditions for successful incubation; (2) proximity to suitable nursery habitat; (3) a location that enables the female to survive for several months for those species that tend the nest site; and (4) for mound-nesting species, the access to suitable vegetative material to build the nest.

All eight species of alligatorids, at least 12 species of true crocodiles, and the false gharial (*Tomistoma schlegelii*) deposit eggs in mounds constructed of vegetation, soil, and woody debris (Grigg & Kirshner, 2015; Figure 1c). The selection of ovipositional sites by these species is influenced to some extent by the presence of suitable ground-layer vegetation that could be utilised as nesting material. In some cases, dense vegetation can conceal nests from predators and overhead canopy cover could buffer against high levels of insolation (Graham, 1981; Harvey & Hill, 2003). Social factors also play a role in nest site selection for highly territorial species such as *Crocodylus porosus*, which avoid nesting in close proximity, especially within visible range (Webb, Manolis, et al., 1983; Webb, Sack, Buckworth, & Manolis, 1983). This behaviour can mean that nest

density is not always related to the availability of vegetation suitable for nest construction and that vegetation structure is a strong driver of population recruitment densities. For example, in open floodplains with low grasses, nests are often located several hundred metres apart in order to provide concealment for the nesting female, while in heavily vegetated swamps (e.g. tall riverine grass that grows c. 2 m tall), female *C. porosus* may nest within c. 10 m of each other if sites are concealed by the grass (M. Brien, personal observation).

## 2.2.2 | Nest materials

Several mound-nesting species of crocodylian, including *A. mississippiensis* (Deitz & Hines, 1980), *C. moreletii* (Platt, Rainwater, Thorbjarnarson, & McMurry, 2008), *A. sinensis* (Platt, Li, He, Wang, & Shunqing, 2016), and *C. porosus* (Webb, Manolis, et al., 1983; Webb, Sack, et al., 1983) are capable of constructing nests out of a broad variety of vegetation types. In captivity, *C. porosus* will even use palm fronds, *Pandanus* leaves, lawn clippings and bale hay when no other vegetation is available (Yangprapakorn, Cronin, & McNeely, 1971; R. Somaweera personal observation; Figure 1d). In areas that have undergone significant urban or agricultural development, *C. porosus* are known to use sugar cane as a nesting material (M. Brien, personal observation), while *A. sinensis* will use pine needles and fern fronds (Thorbjarnarson & Wang, 2010).

If given the choice, however, crocodylians will select for certain vegetation communities in which to locate their nests, and certain vegetation material for which to construct their nests. These choices are often related to the ability to find or construct nests in elevated spots in close proximity to water (Dealaney, 2015; Webb, Messel, & Magnusson, 1977). The structure of the dominant plant species at preferred nest sites is generally similar: long, thick leaves (often grass) and dense enough at the site to be raked into a mound that is tall enough for eggs to be deposited. Furthermore, species such as *A. mississippiensis* and *C. porosus* will often nest in close proximity to a large tree for stability of the nesting spot, elevation, and protection against insolation (Webb et al., 1977).

The type of vegetation available for nest construction significantly influences the composition, size, shape and general appearance of the mounds built by *A. mississippiensis* (Platt, Hastings, & Brantley, 1995), *C. porosus* (Webb, Manolis, et al., 1983; Webb, Sack, et al., 1983) and *C. moreletii* (Platt et al., 2008). These structural differences could have important implications for the thermal environment of the nest mound (e.g. Thorbjarnarson & Wang, 2010), as well as the level of protection from predators, given that larger mounds of more fibrous plants should provide greater resistance to excavation by predators.

The removal or destruction of suitable nesting material, through agriculture, fire or flooding, often results in an absence of nesting at that site, either permanently or until vegetation recovers. For example, along the Adelaide River in northern Australia, mortality of mangrove fern (*Acrostichum speciosum*) due to flooding resulted in no nesting of *C. porosus* in the area until the plants recovered 2–3 years later (C. Manolis, personal observation).

## 2.2.3 | Vegetation change

Regardless of the basis for nest site selection, changes in the vegetation communities in landscapes suitable for nesting may have significant consequences for the viability of crocodylian populations. At a landscape level, introduced plants can modify the local environment and impact crocodylian life histories both directly and indirectly:

1. Prevent access to nesting sites: Invasive and introduced plants in the littoral or riparian zone may limit direct access to nesting substrate by crocodylians (and even other aquatic reptiles such as turtles; Moll & Moll, 2004; Figure 1e). In hole-nesting species, introduced grasses and weeds can prevent females from digging into the substrate (e.g. *C. acutus*, Mazzotti et al., 2009; *C. johnstoni*, Smith, 1987; Webber, Yeoh, & Scott, 2014). In mound-nesting species such as *C. porosus*, the presence of invasive alien vines and shrubs such as *Mimosa pigra* can transform vegetation communities and prevent the growth of native vegetation suitable for nesting (Fukuda, Whitehead, & Boggs, 2007; Leach, Delaney, & Fukuda, 2009; Letnic, 2004; Saalfeld, Fukuda, Duldig, & Fisher, 2015). Platt and Thorbjarnarson (2000) concluded that tropical cyclones in the Caribbean may be important for periodically removing introduced (as well as native) vegetation, and exposing suitable nesting substrate for both *C. acutus* and marine turtles. Nesting female *C. niloticus* at Lake St Lucia in South Africa abandoned previously used and preferred nesting beaches when they encountered fibrous root mats of *Chromolaena odorata* during nest site selection (Leslie & Spotila, 2001).
2. Change physical parameters of the nesting sites: In the U.S.A., the introduced *Melaleuca* spp. can replace open grassy wetlands with forest and may raise soil levels, thus reducing inundation and water flow in *A. mississippiensis* habitats in the Florida Everglades (Mazzotti et al., 2009). Arguably, dominance of weeds in riparian environments around the world that has shallower/poorer root structures relative to native plants makes the banks more susceptible to erosion during flooding. In turn, increased erosion makes nesting areas more prone to disappearing between seasons.
3. Influence sex ratios: Crocodylians have temperature-dependent sex determination. Therefore, the sex of offspring in any 1 year or location depends on a complex interaction between the sites available for oviposition, sites selected for nesting, time of nesting relative to cycles of environmental parameters, and possible long-term selection influences on sex ratio (Webb & Smith, 1984). Cooling (or warming) of nests through shading by vegetation can cause skewed sex ratios, potentially threatening long-term population viability (Berec, Boukal, & Berec, 2001). There is emerging evidence as to how nesting success of crocodylians could also be influenced by the density, abundance, and composition of vegetation within crocodylian habitat. That is, local-scale vegetation change could have impacts at the site or individual nest level. Nesting sites of *C. niloticus* in South Africa shaded by the invasive alien plant Siam weed (*C. odorata*) created soil temperatures

5–6°C below the pivotal temperatures for crocodile eggs, while *C. johnstoni* nests in northern Australia overtopped by the invasive alien vine stinking passionflower (*Passiflora foetida*) had temperature profiles 2–3°C lower than those that were not overtopped (Somaweera, R. and Webber, B.L., unpub. data). Shaded nests of *C. niloticus* have been shown to produce a female-biased sex ratio in the offspring or prevent embryonic development all together (Leslie & Spotila, 2001).

4. Increase embryo mortality: Vegetation nests of *A. sinensis* constructed under introduced pine (*Pinus* spp.) trees in Zhuangtuo, China had pine needles as the predominant nesting material (Thorbjarnarson & Wang, 2010). Pine needles decompose slowly (Gholz, Perry, Cropper, & Hendry, 1985) and produce minimal heat. Although only *prima facie* evidence, one nest reached lethally low temperatures for embryos, resulting in complete nest failure (Thorbjarnarson & Wang, 2010). In northern Australia, the introduced weeds guinea grass (*Panicum maximum*) and para grass (*Brachiaria mutica* spp.) are readily used by wild *C. porosus* as nesting material. However, the use of these materials by captive crocodiles has been observed to increase embryo mortality due to nest over-heating, with nest temperatures reaching up to 36–37°C during decomposition (G. McClure, personal communication, 2017). The introduced weed rubber vine (*Cryptostegia grandiflora*) negatively impacts *C. porosus* nesting in northern Australia by outcompeting vegetation that is more suitable for nest construction. Female crocodiles then have no choice but to use rubber vine for nest material, which results in a loosely composed nest with little protection from sun and predation, leading to higher rates of nest failure (M. Brien, personal observation).

## 2.3 | Communication

### 2.3.1 | Auditory communication

Animals inhabiting complex landscapes modify their signalling to maximise communication effectiveness within different habitat types (Gordon & Uetz, 2011). Vegetation type and density are key factors increasing complexity within most habitats. Crocodylians, such as *A. mississippiensis*, predominantly utilise acoustic signals for communication as they typically occupy densely vegetated habitats where visibility of conspecifics is highly reduced—an indirect relationship between vegetation and communication. In contrast, crocodylian species inhabiting more open waters (e.g. *C. niloticus*) appear to rely more on visual displays for communication (Dinets, 2011b; Garrick & Lang, 1977). However, as demonstrated for the gharial (*Gavialis gangeticus*), distress calls produced at comparatively low frequencies can also occur in crocodylians inhabiting open habitats (Bonke, Whitaker, Roedder, & Boehme, 2015). This use of acoustic communication in relatively open habitats could be a result of intraspecific niche separation. In gharials, adults inhabit deep waters away from littoral vegetation but hatchlings inhabit densely vegetated shallows. Therefore, the alarm system of hatchlings needs to reach the adults over long distances to ensure maternal protection.

Within the same species, populations of crocodylians living in habitats fragmented by shore vegetation use vocal signals more than populations living in continuous aquatic habitats (Dinets, 2011a). However, Dinets (2013) found no evidence that individuals adjust the composition of their signals to habitat parameters, including vegetation change, suggesting that for crocodylians, changes in signal composition are evolved behaviours.

### 2.3.2 | Visual communication

Visual communications such as snout lifting, performed by *C. niloticus* and *C. acutus* inhabiting environments without vegetation, is thought to be more effective when the form and the colour of the head contrast with the aquatic environment (Garrick & Lang, 1977). In the Chambal River, India, adult male gharials have also been observed placing large clumps of floating aquatic vegetation on the end of the snouts (close to the ghar) prior to territorial battles (J. Lang, personal observation). This was interpreted as an attempt by the individual to appear larger, a likely direct use of vegetation in communication.

## 2.4 | Physiology

As ectothermic animals, crocodylians make behavioural adjustments to maintain body temperature within an optimal range. The rise in body temperature is accomplished in part by a combination of heliothermy (basking in the sun) and thigmothermy (absorbing heat from a warm surface; Huey, 1982), either of which could be unavailable, inaccessible or modified in areas with significant vegetation. In such habitats, crocodylians may utilise raised platforms for basking. Climbing into vegetation to presumably improve thermoregulation has been recorded in *A. mississippiensis*, *C. acutus*, *C. palustris*, *C. porosus*, *C. niloticus*, *Crocodylus mindorensis*, *C. siamensis*, *C. johnstoni*, the New Guinea crocodile (*Crocodylus novaeguineae*), the slender-snouted crocodile (*Mecistops cataphractus*), and the dwarf crocodile (*Osteolaemus* sp.; Dinets, Britton, & Shirley, 2013; Van Weerd & Van Der Ploeg, 2012; R. Somaweera personal observation; Figure 1f). Climbing on to overhanging vegetation could presumably also improve surveillance of predators and other crocodylians (Dinets, Britton, & Shirley, 2013).

Vegetation characteristics of the landscape may have also influenced the colouration of crocodylians. On a short-term physiological basis, members of Crocodylidae can rapidly change colour in response to background, potentially for crypsis to evade predators, an ability quite limited in members of Alligatoridae (Merchant, Hale, Brueggen, Harbsmeier, & Adams, 2018). Although, from a long-term natural selection or evolutionary point of view, hatchling crocodylians may have specific colourations that are well-camouflaged and match background vegetation, thus affording a higher degree of protection from aquatic and aerial predators (Hunt & Watanabe, 1982). For example, in *gator holes*, broken grass stems blend with the dorsal yellow bars and light-coloured ventral scales of *A. mississippiensis* hatchlings (Hunt & Watanabe, 1982), and the striped coloration of

*C. porosus* hatchlings also matches surrounding weedy environments (Biddell & Stringer, 1988). Most crocodylians undergo ontogenetic changes to darker, more monochromatic hues as they mature and when the range of potential predators is significantly reduced. Therefore, it is likely that vegetation affects both day-to-day physiological functions of crocodylians as well as long-term evolutionary physiological characteristics.

## 2.5 | Foraging and feeding ecology

Selection of vegetated habitats by young crocodiles may be a function of both increased benefits (e.g. food availability and cover) and reduced costs (e.g. predatory risk; Somaweera et al., 2011). At a landscape level, hatchlings select habitats that are comparatively more vegetated, as they also harbour more prey items (Ouboter & Nanho, 1988; Tamsiripong, 1999; Tucker, Limpus, McCallum, & McDonald, 1996). A study on *C. johnstoni* hatchlings in Australia shows hatchling density was significantly higher in habitats with shoreline and floating vegetation compared to open banks, and both the total number of food items and the total mass of fresh food ingested by hatchlings were positively correlated with hatchling density. Given that hatchlings do not travel far during the early stages, they select vegetated habitats that maximise their feeding rates closer to the nest sites (Somaweera et al., 2011).

At an individual level, crocodylians can have complicated interactions with plants through herbivory, frugivory, saurochory, and the use of plants as tools.

### 2.5.1 | Herbivory and frugivory

It is not unusual for predominantly carnivorous species across all vertebrate groups to occasionally and intentionally consume plant matter as food. For example, during times of food scarcity, lions, leopards, and cheetahs eat moisture-rich plants such as the tsamma melon *Citrullus lanatus* (Bothma 2005; Labuschagne 1979). Several species of neotropical frogs (Da Silva, De Britto-Pereira, & Caramaschi, 1989), lizards (Valido & Olesen, 2007) and even snakes (Engel, 1997; Irvine, 1953; Mookerjee, 1946) that are traditionally considered primarily carnivorous or insectivorous also consume fruits, and some even assist in the dispersal of seeds. It is thus theoretically possible that these carnivorous species *retain* this relict function of feeding on plant matter as a strategy when other food resources are lacking.

Crocodylians are generally considered obligate carnivores, and vegetable matter found among stomach contents is usually attributed to accidental or secondary ingestion (Platt, Elsey, et al., 2013; Platt, Rainwater, Elsey, & Brantley, 2013). However, several studies have found considerable plant matter in the diet of individuals in multiple age classes (Figure 1g) (Thorbjarnarson, 1993; Wallace & Leslie, 2008; Rice, 2004; Webb, Manolis, & Buckworth, 1982; Taylor, 1979; Brito, Andrade, & Abe, 2002). The quantities of plant matter ingested have been too large to be accidental ingestions, with certain plant items also unlikely to be ingested accidentally

(Platt, Rainwater, et al., 2013). Platt, Elsey, et al. (2013) and Platt, Rainwater, et al. (2013) argue that crocodylians probably accrue nutritional benefits from consuming plant matter, as crocodylians are capable of digesting carbohydrates, plant-based proteins and vegetable fats (Coulson, Coulson, Herbert, & Staton, 1987; Staton, 1988). In fact, an experimental study found that alligators can effectively digest plant proteins, and animals that were fed a high plant protein diet showed no clinical signs of plasma biochemistry abnormalities or pathologic changes in liver or kidney function after a 10-month period (Digeronimo et al., 2017).

In a detailed review, Platt, Elsey, et al. (2013) found evidence of frugivory in 13 of 18 (72.2%) species of crocodylians for which dietary information was available. Fruits and seeds have been identified from hatchlings and adult crocodiles (e.g. Platt, Elsey, et al., 2013; Platt, Rainwater, & McMurry, 2002), both in captivity (e.g. Brueggen, 2002; Brito et al., 2002) and in the wild (e.g. Dacey 2012; Forkner 1996). A diversity of plant reproductive structures from 36 plant families was identified from gut contents and scats of crocodylians (Platt, Chenot-Rose, Rose, & Rainwater, 2014; R. Somaweera personal observation; Rainwater, Lowers, Carter, & Platt, 2017). While the majority of these ingestions were viewed as intentional, secondary ingestions (e.g. plant matter found in the bodies of prey of crocodylians) and accidental ingestions cannot be ruled out.

Most fruits float in water and will move around with currents and wind. As crocodylian predatory responses are triggered by movement, the ingestion of at least some of these items in the water may be related to mistaken identity. Crocodylians have been known to attack artificial objects floating and/or moving on water, including those that resemble large fruits (e.g. balls, buoys), which have subsequently been either ingested or have become lodged in the mouth (e.g. *A. mississippiensis* and *C. porosus*: M. Brien, personal observation). Hard seeds may also function as gastroliths (Platt et al., 2002; Staton & Dixon, 1975), especially in habitats where stones are rare or absent (Platt, Brantley, & Hastings, 1990). Additionally, vegetative material, in the form of a knotted ball, has been reported from crocodile stomachs. Wings (2007) referred to these as *bio-gastroliths* but their actual formation, function, or fate remains unknown.

### 2.5.2 | Saurochory

The role of crocodylians in saurochory (seed dispersal by reptiles) has been largely ignored or overlooked by the broader seed dispersal literature (Platt, Elsey, et al., 2013). Given their known frugivorous habits, there is no a priori reason to reject the idea that crocodylians can be an effective disperser of seeds over long distances at a landscape level. Several species of crocodylians are known to move long distances across multiple landscapes and even oceans (Campbell et al., 2010; Rosenblatt & Heithaus, 2011). Arguably ingestion by crocodylians may provide seeds with protection against damaging salt water on inter-continental journeys. However, to be an effective seed dispersal agent, crocodylians must not only transport seeds but the seeds must also remain viable and capable of germination after being expelled. In the only study to test germination of ingested

seeds, Rosenblatt, Zona, Heithaus, and Mazzotti (2014) found that 20 pond apple (*Annona glabra*) seeds from the stomach of a single *A. mississippiensis* were non-viable under ideal germination conditions, although fresh and non-digested pond apple seeds were highly viable under the same conditions. The authors suggest that seeds are probably destroyed in the highly acidic gastric environment, and therefore, alligators are likely to function as seed predators, rather than seed dispersers. However, given that the limited sample size came from one gut-passage event and the seeds were stored before being planted, it may not be appropriate to generalise the findings.

### 2.5.3 | Tools in hunting

Anecdotal observations may support the notion that crocodylians intentionally or unintentionally use vegetation as tools for either camouflage or as lures during hunting. Use of tools as hunting lures is known among mammals and birds (Bentley-Condit & Smith, 2010), but had not been documented among reptiles until recently (e.g. Shumaker, Walkup, & Beck, 2011) anecdotally reported a case of *C. porosus* seemingly using fish fragments to attract birds). Opportunistic observations of captive *A. mississippiensis* and *C. palustris* placing sticks on their snouts have been interpreted as tool use to lure nesting wading birds into striking distance (Dinets, Brueggen, & Brueggen, 2013). *Alligator mississippiensis* in FL, U.S.A., floated in a pond with sticks balanced across their snouts, while *C. palustris* in Chennai, India, lay in shallow water along the edge of the pond with sticks and twigs positioned across their snouts (Dinets, Brueggen, & Brueggen, 2013). In both cases, wading bird rookeries were located nearby and the birds were actively searching for sticks and twigs for nest construction. The nesting birds approached the crocodylians to collect the sticks from the top of their snouts, and the crocodylians would lunge at the birds, with successful predation observed in *A. mississippiensis*. These observations provide *prima facie* evidence of a systematic approach to improving hunting success, but confirmation would require controlled studies to determine if the luring attempts were deliberate. For example, the placement of sticks on by the crocodiles could merely be incidental, as crocodylians emerging from water can remain covered by plant matter (Figure 1h).

## 3 | FROM UNDERSTANDING INTERACTIONS TO MANAGING IMPACTS

Currently, half of the world's crocodylian species are considered to be threatened with extinction (IUCN, 2017). Direct impacts, including killing for skins and meat and also through the human-crocodile conflict, are a major contributor to population declines globally. By contrast, accelerated and extensive anthropogenic modification of environments is causing significant changes in global vegetation. We have shown here that the inter-dependencies are considerable between crocodiles and the vegetative elements of the communities they occupy. Many of these interactions remain poorly understood, yet the possible consequences could be considerable from

a conservation perspective. Rapid global environmental change can transform habitats and alter threats at rates never before experienced and can often involve tipping points beyond which recovery is extremely challenging at best. Because of their cryptic nature and long lifespans, combined with limited knowledge on demographic trajectories (e.g. population counts rarely include juveniles), there is a high risk that global environmental change threatens to crocodylians will remain undetected unless given explicit consideration.

There is some evidence to suggest that certain crocodylians can survive in highly disturbed habitats and still reproduce to maintain viable populations (Brandt et al., 1995; Evans, Jones, Pang, Saimin, & Goossens, 2016), but the long-term impacts of such disturbances on population recruitment (and therefore population fitness and stability) are rarely considered. Loss and degradation of riparian and wetland vegetation essential for nesting, hatchling survivorship and as living spaces are a common threat to all crocodylians and have been documented for populations of almost all crocodylians (Martin, 2008; Seijas & Chavez, 2000; Shirley, Oduro, & Beibro, 2009).

If we are to be able to factor in global environmental change drivers into prioritised, evidence-based decisions for the conservation of crocodylians, then there are large knowledge gaps that need to be addressed. We have shown here that many of these knowledge gaps relate to the interactions between crocodylians and the vegetative elements of their environment. Factors such as nest site and habitat selection, thermoregulation, feeding and communication are all influenced and have evolved as adaptations to local vegetation, and these factors are driven both directly and indirectly by vegetation-related interactions. A growing body of evidence shows that changes to aquatic and littoral vegetation could have significant impacts on crocodiles at the population level (Bezuijen et al., 2013; González-Trujillo et al., 2014). We conclude by highlighting two priority areas where new knowledge will contribute the greatest gains to conservation outcomes for crocodylians.

Firstly, significant knowledge gaps still exist in regard to the role of vegetation in crocodylian nest site selection. Our understanding of what characteristics of vegetation communities (or habitats) distinguish those suitable for nest site selection from those unsuitable is still rudimentary, especially in highly dynamic habitats such as river floodplains.

Secondly, apart from direct human-mediated destruction of vegetation communities, changes are also caused indirectly by invasive pests and weeds. Our understanding of how changes caused by invasive plants and animals to vegetation structure and composition affect crocodylians over the long-term is substantially limited. Introduced feral water buffalo (*Bubalus bubalis*), and also cattle to a lesser extent, have caused significant declines in plant communities used for nesting by *C. porosus* through severe trampling and over grazing in several river systems in northern Australia. This occurred to the extent that no crocodile nests were observed until the buffalos were removed and vegetation regenerated at the sites (Hill & Webb, 1982; Webb et al., 1977). In contrast, in Cambodia where most large mammals including wild water buffalo are extinct, aquatic

mats have proliferated exponentially making it difficult for *C. siamensis* to access potential nesting sites (S. Platt, personal observation). The introduced omnivorous fish pacu (*Piaractus brachupomum*) and Java bard (*Puntius gonionotus*) damage the floating mats of vegetation used for *C. porosus* nesting in Papua New Guinea causing potential declines in the populations (Cox et al., 2006; UNDP, 2012). To find a balance between conservation and production values, we need to understand how to best mitigate pest, weed and agricultural impacts on global crocodylian populations, particularly in areas where critically endangered species of crocodylians occur in poorly managed environments, to find a balance between conservation and production values.

The cryptic and aquatic lifestyles of crocodylians make it difficult to observe interactions with other components of the environment, and their long lifespans create a lag time of detecting changes to populations. A better understanding of these complicated synergies (often with slow change trajectories) will be essential for implementing more effective, evidence-based management actions against global environmental change drivers.

## ACKNOWLEDGMENTS

We are grateful to Bruce Shwedick, Steve Gorzula, Marisa Tellez, Jeff Lang, Mitch Eaton, Thomas Rainwater, Grahame Webb, Shawn K. Heflick, Allan R. Woodward, Asghar Mobaraki, Deb Levinson, Lewis Medlock, Ruth Elsey, Phil Wilkinson, Patrick Delaney and Subir Chowfin for sharing literature and providing personal comments. This research is part of a program of work on crocodylian ecology and invasive plant management funded through the Australian Government's National Environmental Science Programme.

## AUTHORS' CONTRIBUTIONS

R.S. and B.L.W. conceived the ideas and designed the framework; R.S., M.L.B., C.M., and S.G.P. did the literature review; R.S., S.G.P., and B.L.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## ORCID

Ruchira Somaweera  <http://orcid.org/0000-0002-7470-8736>

## REFERENCES

- Álvarez Del Toro, M. (1974). *Los crocodylia de México: Estudio comparativo*. México City, Mexico: Instituto Mexicano de Recursos Naturales Renovables, AC.
- Ashton, P. J. (2010). The demise of the Nile crocodile (*Crocodylus niloticus*) as a keystone species for aquatic ecosystem conservation in South Africa: The case of the Olifants River. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 20, 489–493. <https://doi.org/10.1002/aqc.1132>
- Bates, L. A., & Byrne, R. W. (2007). Creative or created: Using anecdotes to investigate animal cognition. *Methods*, 42, 12–21. <https://doi.org/10.1016/j.ymeth.2006.11.006>
- Bentley-Condit, V. K., & Smith, E. (2010). Animal tool use: Current definitions and an updated comprehensive catalog. *Behaviour*, 147(2), 185–221.
- Berec, L., Boukal, D. S., & Berec, M. (2001). Linking the Allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. *The American Naturalist*, 157, 217–230.
- Bezuijen, M. R., Cox, J. H. Jr, Thorbjarnarson, J. B., Phohtitay, C., Hedemark, M., & Rasphone, A. (2013). Status of Siamese crocodile (*Crocodylus siamensis*) Schneider, 1801 (Reptilia: Crocodylia) in Laos. *Journal of Herpetology*, 47, 41–65. <https://doi.org/10.1670/11-157>
- Biddell, G., & Stringer, C. (1988). *Crocodyles of Australia*. Darwin, NT, Australia: Adventure Publications.
- Bonke, R., Whitaker, N., Roedder, D., & Boehme, W. (2015). Vocalizations in two rare crocodylian species: A comparative analysis of distress calls of *Tomistoma schlegelii* (Müller, 1838) and *Gavialis gangeticus* (Gmelin, 1789). *North-Western Journal of Zoology*, 11, 151–162.
- Bothma, J. D. P. (2005). Water-use by southern Kalahari leopards. *South African Journal of Wildlife Research*, 35, 131–137.
- Brandt, L. A., Mazzotti, F. J., Wilcox, J. R., Barker, P. D., Hasty, G. L., & Wasilewski, J. (1995). Status of the American crocodile (*Crocodylus acutus*) at a power plant site in Florida, USA. *Herpetological Natural History*, 3, 29–36.
- Brazaitis, P., & Watanabe, M. E. (2011). Crocodylian behaviour: A window to dinosaur behaviour? *Historical Biology*, 23, 73–90. <https://doi.org/10.1080/08912963.2011.560723>
- Brito, S. P., Andrade, D. V., & Abe, A. S. (2002). Do caimans eat fruit. *Herpetological Natural History*, 9, 95–96.
- Brueggen, J. (2002). Crocodylians eating their vegetables. *IUCN Crocodile Specialists Group Newsletter*, 21, 16.
- Caldwell, J. (2017). *World trade in crocodylian skins 2013-2015*. In *Prepared as part of the International alligator and crocodile trade study* (p. 32). Cambridge, UK: UNEP-WCMC.
- 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, 955–964. <https://doi.org/10.1111/j.1365-2656.2010.01709.x>
- Cedeño-Vázquez, J. R., Ross, J. P., & Calmé, S. (2006). Population status and distribution of *Crocodylus acutus* and *C. moreletii* in southeastern Quintana Roo, Mexico. *Herpetological Natural History*, 10, 17–30.
- Conn, V. S., Valentine, J. C., Cooper, H. M., & Rantz, M. J. (2003). Grey literature in meta-analyses. *Nursing Research*, 52, 256–261. <https://doi.org/10.1097/00006199-200307000-00008>
- Cott, H. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *The Transactions of the Zoological Society of London*, 29, 211–356.
- Coulson, R. A., Coulson, T. D., Herbert, J. D., & Staton, M. A. (1987). Protein nutrition in the alligator. *Comparative Biochemistry and Physiology Part A: Physiology*, 87, 449–459. [https://doi.org/10.1016/0300-9629\(87\)90150-2](https://doi.org/10.1016/0300-9629(87)90150-2)
- Cox, J., Gowep, B., Mava, A., Wana, J., Genolagani, J., Kula, V., ... Langelet, E. (2006). The saltwater crocodile, *Crocodylus porosus*, egg harvest program in Papua New Guinea: linking conservation, commerce and community development. In *Crocodyles, Proceedings of the 18th working meeting of the Crocodile Specialist Group* (pp. 134–155). Gland, Switzerland.
- Dacey, T. (2012). Summary report on a visit to Lao PDR. *IUCN Crocodile Specialists Group Newsletter*, 31, 6–8.
- Da Silva, H. R., De Britto-Pereira, M. C., & Caramaschi, U. (1989). Frugivory and seed dispersal by *Hyla truncata*, a neotropical treefrog. *Copeia*, 1989, 781–783. <https://doi.org/10.2307/1445517>
- Da Silveira, R., Magnusson, W. E., & Campos, Z. (1997). Monitoring the distribution, abundance and breeding areas of *Caiman crocodylus* and *Melanosuchus niger* in the Anavilhanas Archipelago,

- Central Amazonia, Brazil. *Journal of Herpetology*, 31, 514–520. <https://doi.org/10.2307/1565603>
- De Silva, A. (2013). *The crocodiles of Sri Lanka: Including archeology, history, folklore, traditional medicine, human-crocodile conflict and a bibliography of the literature on crocodiles of Sri Lanka*. Gampola, Sri Lanka: Author.
- Dealaney, J. P. (2015). *Scale-dependent nest site selection by American alligators (Alligator mississippiensis) in three central Florida lakes*. MSc. : University of Florida.
- Deitz, D. C., & Hines, T. C. (1980). Alligator nesting in North-Central Florida. *Copeia*, 1980, 249–258. <https://doi.org/10.2307/1444001>
- Deraniyagala, P. E. P. (1939). *The tetrapod reptiles of Ceylon. Vol. 1 Testudinates and crocodylians*. Colombo, Sri Lanka: Ceylon National Museum.
- Dever, J. A., Strauss, R. E., Rainwater, T. R., McMurry, S. T., & Densmore Iii, L. D. (2002). Genetic diversity, population subdivision, and gene flow in Morelet's crocodile (*Crocodylus moreletii*) from Belize, Central America. *Copeia*, 2002, 1078–1091. [https://doi.org/10.1643/0045-8511\(2002\)002\[1078:gdpsag\]2.0.co;2](https://doi.org/10.1643/0045-8511(2002)002[1078:gdpsag]2.0.co;2)
- Digeronimo, P. M., Di Girolamo, N., Crossland, N. A., Del Piero, F., Reigh, R. C., & Nevarez, J. G. (2017). Effects of plant protein diets on the health of farmed American alligators (*Alligator mississippiensis*). *Journal of Zoo and Wildlife Medicine*, 48, 131–135. <https://doi.org/10.1638/2016-0067.1>
- Dinets, V. (2011a). Effects of aquatic habitat continuity on signal composition in crocodylians. *Animal Behaviour*, 82, 191–201. <https://doi.org/10.1016/j.anbehav.2011.04.012>
- Dinets, V. (2011b). *The role of habitat in crocodylian communication*. PhD. University of Miami.
- Dinets, V. (2013). Do individual crocodylians adjust their signaling to habitat structure? *Ethology Ecology and Evolution*, 25, 174–184. <https://doi.org/10.1080/03949370.2012.744358>
- Dinets, V., Britton, A., & Shirley, M. (2013). Climbing behaviour in extant crocodylians. *Herpetology Notes*, 7, 3–7.
- Dinets, V., Brueggen, J. C., & Brueggen, J. D. (2013). Crocodylians use tools for hunting. *Ethology Ecology and Evolution*, 27, 74–78.
- Engel, T. R. (1997). Seed dispersal and plant regeneration by snakes. *Ecotropica*, 3, 33–41.
- Evans, L. J., Jones, T. H., Pang, K., Saimin, S., & Goossens, B. (2016). Spatial ecology of estuarine crocodile (*Crocodylus porosus*) nesting in a fragmented landscape. *Sensors*, 16, 1527. <https://doi.org/10.3390/s16091527>
- Forkner, B. (Ed.) (1996). *John James Audubon: selected journals and other writings*. New York: Penguin Books.
- Fukuda, Y., Webb, G., Manolis, C., Delaney, R., Letnic, M., Lindner, G., & Whitehead, P. (2011). Recovery of saltwater crocodiles following unregulated hunting in tidal rivers of the Northern Territory, Australia. *The Journal of Wildlife Management*, 75, 1253–1266. <https://doi.org/10.1002/jwmg.191>
- Fukuda, Y., Whitehead, P., & Boggs, G. (2007). Broad-scale environmental influences on the abundance of saltwater crocodiles (*Crocodylus porosus*) in Australia. *Wildlife Research*, 34, 167–176. <https://doi.org/10.1071/wr06110>
- Garrick, L. D., & Lang, J. W. (1977). Social signals and behaviors of adult alligators and crocodiles. *American Zoologist*, 17, 225–239. <https://doi.org/10.1093/icb/17.1.225>
- Gholz, H. L., Perry, C., Cropper, W., & Hendry, L. (1985). Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (*Pinus elliottii*) plantations. *Forest Science*, 31, 463–478.
- Glastra, R. (1983). Notes on a population of *Caiman crocodylus crocodylus* depleted by hide hunting in Surinam. *Biological Conservation*, 26, 149–162. [https://doi.org/10.1016/0006-3207\(83\)90063-0](https://doi.org/10.1016/0006-3207(83)90063-0)
- González-Trujillo, R., Méndez-Alonzo, R., Arroyo-Rodríguez, V., Vega, E., González-Romero, A., & Reynoso, V. H. (2014). Vegetation cover and road density as indicators of habitat suitability for the Morelet's crocodile. *Journal of Herpetology*, 48, 188–194. <https://doi.org/10.1670/12-150>
- Gordon, S. D., & Uetz, G. W. (2011). Multimodal communication of wolf spiders on different substrates: Evidence for behavioural plasticity. *Animal Behaviour*, 81, 367–375. <https://doi.org/10.1016/j.anbehav.2010.11.003>
- Graham, A. (1981). *Mapping the pattern of crocodile nesting activity in Papua New Guinea*. Port Moresby, Papua New Guinea: Wildlife Division, Department of Lands and Environment, Food and Agriculture Organization of the United Nations.
- Grigg, G., & Kirshner, D. (2015). *Biology and evolution of crocodylians*. Clayton, Vic., Australia: CSIRO Publishing.
- Harvey, K. R., & Hill, G. J. (2003). Mapping the nesting habitats of saltwater crocodiles (*Crocodylus porosus*) in Melacca Swamp and the Adelaide River wetlands, Northern Territory: An approach using remote sensing and GIS. *Wildlife Research*, 30, 365–375. <https://doi.org/10.1071/wr00008>
- Hill, R., & Webb, G. (1982). Floating grass mats of the Northern Territory floodplains—an endangered habitat? *Wetlands Australia Journal*, 2, 45–50.
- Honegger, R.E. (1971). *The status of four threatened crocodylian species of Asia*. In: Proceedings of the first working meeting of Crocodile Specialists sponsored by the New York Zoological Society and organized by the Survival Service Commission, IUCN, at the Bronx Zoo. IUCN.
- Huey, R.B. (1982). Temperature, physiology, and the ecology of reptiles. In C. Gans & F. H. Pough (Eds.), *Biology of the reptilia*, Vol. 12 (pp. 93–166). New York, NY: Academic Press. CiteSeer.
- Hunt, R. H., & Watanabe, M. E. (1982). Observations on maternal behavior of the American alligator, *Alligator mississippiensis*. *Journal of Herpetology*, 16, 235–239. <https://doi.org/10.2307/1563716>
- Irvine, F. (1953). Herbivorous snakes. *British Journal of Herpetology*, 1, 173.
- IUCN (2017). *The IUCN red list of threatened species*. Version 2017-3. Retrieved from <http://www.iucnredlist.org>. Downloaded on 29 January 2018.
- Kofron, C. P. (1992). Status and habitats of the three African crocodiles in Liberia. *Journal of Tropical Ecology*, 8, 265–273. <https://doi.org/10.1017/s0266467400006490>
- Kushlan, J. A. (1974). Observations on the role of the American alligator (*Alligator mississippiensis*) in the southern Florida wetlands. *Copeia*, 1974, 993–996. <https://doi.org/10.2307/1442609>
- Kushlan, J. A., & Mazzotti, F. J. (1989a). Historic and present distribution of the American crocodile in Florida. *Journal of Herpetology*, 23, 1–7. <https://doi.org/10.2307/1564309>
- Kushlan, J. A., & Mazzotti, F. J. (1989b). Population biology of the American crocodile. *Journal of Herpetology*, 23, 7–21. <https://doi.org/10.2307/1564310>
- Labuschagne, W. (1979). *Bio-ekologiese en gedragstudie van die jagluiperd Acinonyx jubatus jubatus (Schreber, 1776)*. MSc Dissertation, University of Pretoria, Pretoria.
- Lang, J. W. (1987). Crocodylian behaviour: Implications for management. In G. J. W. Webb, S. C. Manolis, & P. J. Whitehead (Eds.), *Wildlife management: Crocodiles and alligators* (pp. 273–294). Sydney, NSW, Australia: Surrey Beatty.
- Leach, G., Delaney, R., & Fukuda, Y. (2009). *Management program for the saltwater crocodile in the Northern Territory of Australia, 2009–2014*. Darwin, NT, Australia: Department of Natural Resources, Environment, the Arts and Sport.
- Leslie, A.J., & Spotila, J.R. (2001). Alien plant threatens Nile crocodile (*Crocodylus niloticus*) breeding in Lake St. Lucia, South Africa. *Biological Conservation*, 98, 347–355. [https://doi.org/10.1016/s0006-3207\(00\)00177-4](https://doi.org/10.1016/s0006-3207(00)00177-4)
- Letnic, M. (2004). *Crocodile management in the Northern Territory of Australia*. In *Crocodiles: Proceedings of the 17th Working Meeting of the*

- IUCN-SSC Crocodile Specialist Group (pp. 4–12). Darwin, NT, Australia. Gland, Switzerland: IUCN.
- Magnusson, W. E., Lima, A. P., & Sampaio, R. M. (1984). Sources of heat for nests of *Paleosuchus trigonatus* and a review of crocodylian nest temperatures. *Journal of Herpetology*, *19*, 199–207.
- Martin, S. (2008). Global diversity of crocodyles (Crocodylia, Reptilia) in freshwater. *Hydrobiologia*, *595*, 587–591.
- Mazzotti, F. J. (1999). The American crocodile in Florida Bay. *Estuaries and Coasts*, *22*, 552–561. <https://doi.org/10.2307/1353217>
- 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*, 137–149. <https://doi.org/10.1016/j.ecolind.2008.06.008>
- Mazzotti, F. J., Brandt, L. A., Moler, P., & Cherkiss, M. S. (2007). American crocodile (*Crocodylus acutus*) in Florida: Recommendations for endangered species recovery and ecosystem restoration. *Journal of Herpetology*, *41*, 122–132. [https://doi.org/10.1670/0022-1511\(2007\)41\[122:accaif\]2.0.co;2](https://doi.org/10.1670/0022-1511(2007)41[122:accaif]2.0.co;2)
- Mazzotti, F.J., Cherkiss, M.S., Parry, M.W., & Rice, K.G. (2007). Recent nesting of the American crocodile *Crocodylus acutus* in Everglades National Park, Florida, USA. *Herpetological Review*, *38*, 285–289.
- Merchant, M., Hale, A., Brueggen, J., Harbsmeier, C., & Adams, C. (2018). Crocodiles alter skin color in response to environmental color conditions. *Scientific Reports*, *8*, 6174. <https://doi.org/10.1038/s41598-018-24579-6>
- Moll, D., & Moll, E.O. (2004). *The ecology, exploitation and conservation of river turtles*. Oxford, UK: Oxford University Press on Demand.
- Mookerjee, S. (1946). Mango fruit on the menu of the common python (*Python molurus*). *Journal of the Bombay Natural History Society*, *46*, 733.
- Nifong, J. (2018). Ecological value of crocodylians. In *Crocodylian capacity building manual*, Vol. 26. IUCN-SSC Crocodile Specialist Group. Retrieved from <http://www.iucnscg.org/pages/Crocodylian-Capacity-Building-Manual-Home.html>
- Olupona, J. K. (1993). Some notes on animal symbolism in African religion and culture. *Anthropology and Humanism*, *18*, 3–12. <https://doi.org/10.1525/ahu.1993.18.1.3>
- Ouboter, P. E., & Nanho, L. M. R. (1988). Habitat selection and migration of *Caiman crocodylus crocodylus* in a swamp and swamp-forest habitat in northern Suriname. *Journal of Herpetology*, *22*, 283–294. <https://doi.org/10.2307/1564151>
- Palmer, M. L., & Mazzotti, F. J. (2004). Structure of Everglades alligator holes. *Wetlands*, *24*, 115–122. [https://doi.org/10.1672/0277-5212\(2004\)024\[0115:soeah\]2.0.co;2](https://doi.org/10.1672/0277-5212(2004)024[0115:soeah]2.0.co;2)
- Parker, I. (1970). Crocodile distribution and status in the major waters of western and central Uganda in 1969. *African Journal of Ecology*, *8*, 85–103. <https://doi.org/10.1111/j.1365-2028.1970.tb00833.x>
- Passariello, P. (1999). Me and my totem: Cross-cultural attitudes towards animals. In F.L. Dolins (Ed.), *Attitudes to animals: Views in animal welfare* (pp. 12–25). Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/cbo9780511608476>
- Platt, S. (2000). Dens and denning behavior of Morelet's crocodile (*Crocodylus moreletii*). *Amphibia-Reptilia*, *21*, 232–237.
- Platt, S. G., Brantley, C. G., & Hastings, R. W. (1990). Food habits of juvenile American Alligators in the upper Lake Pontchartrain estuary. *Northeast Gulf Science*, *11*, 123–130.
- Platt, S. G., Chenot-Rose, C., Rose, V., & Rainwater, T. R. (2014). *Crocodylus acutus* (American crocodile) frugivory. *Herpetological Review*, *45*, 120–121.
- Platt, S. G., Elsey, R. M., Liu, H., Rainwater, T. R., Nifong, J. C., Rosenblatt, A. E., ... Mazzotti, F. J. (2013). Frugivory and seed dispersal by crocodylians: An overlooked form of saurochory? *Journal of Zoology*, *291*, 87–99. <https://doi.org/10.1111/jzo.12052>
- Platt, S.G., Hastings, R.W. & Brantley, C.G. (1995). Nesting ecology of the American alligator in Southeastern Louisiana. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies*, *49*, 629–639.
- Platt, S. G., Li, F., He, Q., Wang, J., & Shunqing, L. (2016). Reproduction in a reintroduced population of Chinese alligators. *CSG newsletter*, *35*, 11–15.
- Platt, S. G., Rainwater, T. R., Elsey, R. M., & Brantley, C. G. (2013). Canebrake fauna revisited: Additional records of species diversity in a critically endangered ecosystem. *The Journal of the American Bamboo Society*, *26*, 1–12.
- Platt, S. G., Rainwater, T. R., & McMurry, S. T. (2002). Diet, gastrolith acquisition and initiation of feeding among hatchling Morelet's crocodiles in Belize. *Herpetological Journal*, *12*, 81–84.
- Platt, S. G., Rainwater, T. R., Thorbjarnarson, J. B., & McMurry, S. T. (2008). Reproductive dynamics of a tropical freshwater crocodylian: Morelet's crocodile in northern Belize. *Journal of Zoology*, *275*, 177–189. <https://doi.org/10.1111/j.1469-7998.2008.00426.x>
- Platt, S. G., & Thorbjarnarson, J. B. (2000). Status and conservation of the American crocodile, *Crocodylus acutus*, in Belize. *Biological Conservation*, *96*, 13–20. [https://doi.org/10.1016/S0006-3207\(00\)00038-0](https://doi.org/10.1016/S0006-3207(00)00038-0)
- Rainwater, T. R., Lowers, R. H., Carter, C., & Platt, S. G. (2017). *Alligator mississippiensis* (American alligator) frugivory. *Herpetological Review*, *48*, 430–431.
- Rajbhandari, S. L., & Acharya, P. M. (2014). Habitat use and conservation of marsh crocodile (*Crocodylus palustris*, Lesson, 1831) in Beeshazari lake complex, Nepal. *Journal of Indian Research*, *2*, 40–48.
- Refsnider, J. M. (2016). Nest-site choice and nest construction in non-avian reptiles: evolutionary significance and ecological implications. *Avian Biology Research*, *9*, 76–88.
- Rice, A. N. (2004). *Diet and condition of American alligators (Alligator mississippiensis) in three central Florida lakes*. MSc. University of Florida.
- Rootes, W. L., & Chabreck, R. H. (1993). *Cannibalism in the American alligator*. *Herpetologica*, *49*, 99–107.
- Rosenblatt, A. E., & Heithaus, M. R. (2011). Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *Journal of Animal Ecology*, *80*, 786–798. <https://doi.org/10.1111/j.1365-2656.2011.01830.x>
- Rosenblatt, A. E., Zona, S., Heithaus, M. R., & Mazzotti, F. J. (2014). Are seeds consumed by crocodylians viable? A test of the crocodylian saurochory hypothesis. *Southeastern Naturalist*, *13*, N26–N29. <https://doi.org/10.1656/058.013.0304>
- Ross, J. (1995). La importancia del uso sustentado para la conservación de los cocodrilos. In A. Larriera & L. M. Verdade (Eds.), *La conservación y el manejo de caimanes y cocodrilos de América Latina* (pp. 19–32). Santo Tomé, Santa Fe, Argentina: Fundación Banco Bica.
- Ross, J.P. (1998). *Crocodyles. Status survey and conservation action plan* (p. 167, Viii+). Gland, Switzerland and Cambridge, UK: IUCN/SSC Crocodile Specialist Group, IUCN.
- Saalfeld, K., Fukuda, Y., Duldig, T., & Fisher, A. (2015). *Wildlife trade management plan for the saltwater crocodile (Crocodylus porosus) in the Northern Territory of Australia, 2016–2020*. Darwin, NT, Australia: Northern Territory Department of Land Resource Management.
- Safina, C. (2015). *Beyond words: What animals think and feel*. London, UK: Picador.
- Seijas, A. E., & Chavez, C. (2000). Population status of the Orinoco crocodile (*Crocodylus intermedius*) in the Cojedes river system, Venezuela. *Biological Conservation*, *94*, 353–361. [https://doi.org/10.1016/S0006-3207\(99\)00184-6](https://doi.org/10.1016/S0006-3207(99)00184-6)
- Seymour, R. S., Bennett-Stamper, C. L., Johnston, S. D., Carrier, D. R., & Grigg, G. C. (2004). Evidence for endothermic ancestors of crocodylians at the stem of archosaur evolution. *Physiological and Biochemical Zoology*, *77*, 1051–1067. <https://doi.org/10.1086/422766>
- Shirley, M. H., Oduro, W., & Beibro, H. Y. (2009). Conservation status of crocodylians in Ghana and Cote-d'Ivoire, West Africa. *Oryx*, *43*, 136–145. <https://doi.org/10.1017/S0030605309001586>
- Shumaker, R.W., Walkup, K.R., & Beck, B.B. (2011). *Animal tool behavior: The use and manufacture of tools by animals*. Baltimore, MD: Johns Hopkins Press.

- Simkhada, P., Knight, J., Reid, G., Wyness, L., & Mandava, L. (2005). *Chasing the grey evidence: A standardised systematic critical literature review approach*. Edited by D. J. Farace (pp. 91–93). Aberdeen: University of Aberdeen.
- Simpson, B. (2006). *Siamese crocodile survey and monitoring handbook: An introduction for conservation workers in Cambodia*. Fauna & Flora International, Cambodia Programme.
- Skinner, H. D. (1964). *Crocodile and lizard in New Zealand myth and material culture*. Dunedin, New Zealand: Otago Museum Trust Board.
- Smith, A. M. A. (1987). *The sex and survivorship of embryos and hatchlings of the Australian freshwater crocodiles, Crocodylus johnstoni*. PhD. Canberra, ACT: Australian National University.
- 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, 72–79.
- Somaweera, R., Brien, M., & Shine, R. (2013). The role of predation in shaping crocodylian natural history. *Herpetological Monographs*, 27, 23–51. <https://doi.org/10.1655/herpmonographs-d-11-00001>
- Somaweera, R., Webb, J. K., & Shine, R. (2011). Determinants of habitat selection by hatchling Australian freshwater crocodiles. *PLoS ONE*, 6, e28533. <https://doi.org/10.1371/journal.pone.0028533>
- Staton, M. A. (1988). *Studies on the use of fats and carbohydrates in the diet of American alligators (Alligator mississippiensis)*. PhD. University of Georgia.
- Staton, M.A. (1989). *A literature-based study on the relationships between alligators and alligator habitats* (p. 112). Austin, TX: Texas Parks and Wildlife Department.
- Staton, M. A., & Dixon, J. R. (1975). Studies on the dry season biology of *Caiman crocodilus crocodilus* from the Venezuelan Llanos. *Memoria de la Sociedad de Ciencias Naturales La Salle*, 35, 237–265.
- Steel, R. (1989). *Crocodyles*. Dundee: Christopher Helm.
- Taylor, J. A. (1979). The foods and feeding habits of subadult *Crocodylus porosus* Schneider in northern Australia. *Wildlife Research*, 6, 347–359. <https://doi.org/10.1071/wr9790347>
- Temsiripong, Y. (1999). *Growth and survival rates of wild and repatriated hatchling American alligators (Alligator mississippiensis) in Central Florida lakes*. MSc.
- Thorbjarnarson, J. B. (1993). Diet of the spectacled caiman (*Caiman crocodilus*) in the Central Venezuelan Llanos. *Herpetologica*, 49, 108–117.
- Thorbjarnarson, J. (1999). Crocodile tears and skins: International trade, economic constraints, and limits to the sustainable use of crocodylians. *Conservation Biology*, 13, 465–470. <https://doi.org/10.1046/j.1523-1739.1999.00011.x>
- Thorbjarnarson, J. B., & Hernández, G. (1992). Recent investigations of the status and distribution of the Orinoco crocodile *Crocodylus intermedius* in Venezuela. *Biological Conservation*, 62, 179–188. [https://doi.org/10.1016/0006-3207\(92\)91046-u](https://doi.org/10.1016/0006-3207(92)91046-u)
- Thorbjarnarson, J., & Wang, X. (2010). *The Chinese alligator: Ecology, behavior, conservation, and culture*. Baltimore, MD: JHU Press.
- Thorbjarnarson, J., Wang, X. M., & He, L. J. (2001). Reproductive ecology of the Chinese alligator (*Alligator sinensis*) and implications for conservation. *Journal of Herpetology*, 35, 553–558. <https://doi.org/10.2307/1565892>
- Thorbjarnarson, J. (1989). Ecology of the American crocodile, *Crocodylus acutus*. In P. Hall, & R. Bryant (Eds.), *Crocodyles: Their ecology, management and conservation* (pp. 228–258). Gland, Switzerland: IUCN.
- Tucker, A. D., Limpus, C. J., McCallum, H. I., & McDonald, K. R. (1996). Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. *Copeia*, 1996, 978–988. <https://doi.org/10.2307/1447661>
- UNDP (2012). *Sepik wetlands management initiative*. Papua New Guinea. *Equator Initiative Case Study Series*. New York, NY: UNDP.
- Valido, A., & Olesen, J. M. (2007). *The importance of lizards as frugivores and seed dispersers*. Wallingford: CAB International. <https://doi.org/10.1079/9781845931650.0000>
- Van Weerd, M., & Van Der Ploeg, J. (2012). *The Philippine crocodile: Ecology, culture and conservation* (p. 36). Cabagan, Philippines: Mabuwaya Foundation.
- Villegas, A., & Reynoso, V.H. (2013). Relative abundance and habitat preference in isolated populations of Morelet's crocodile (*Crocodylus moreletii*) along the coast of the Gulf of Mexico. *Herpetological Conservation and Biology*, 8, 571–580.
- Wallace, K. M., & Leslie, A. J. (2008). Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology*, 42, 361–368. <https://doi.org/10.1670/07-1071.1>
- Wallach, A. D., Izhaki, I., Toms, J. D., Ripple, W. J., & Shanas, U. (2015). What is an apex predator? *Oikos*, 124, 1453–1461. <https://doi.org/10.1111/oik.01977>
- Walsh, B. (1989). Aestivation in the Australian freshwater crocodile? *Australian Zoologist*, 25, 68–70. <https://doi.org/10.7882/az.1989.004>
- Webb, G. (2014). *Wildlife conservation: In the belly of the beast*. Darwin, NT, Australia: Charles Darwin University Press.
- Webb, G. J. W., Manolis, S. C., & Buckworth, R. (1982). *Crocodylus johnstoni* in the McKinlay River area, N.T. I. Variation in the diet, and a new method of assessing the relative importance of prey. *Australian Journal of Zoology*, 30, 877–899. <https://doi.org/10.1071/zo9820877>
- Webb, G. J. W., Manolis, S. C., & Sack, G. C. (1983). *Crocodylus johnstoni* and *C. porosus* coexisting in a tidal river. *Australian Wildlife Research*, 10, 639–650. <https://doi.org/10.1071/wr9830639>
- Webb, G. J. W., Messel, H., & Magnusson, W. (1977). The nesting of *Crocodylus porosus* in Arnhem Land, Northern Australia. *Copeia*, 1977, 238–249. <https://doi.org/10.2307/1443905>
- Webb, G. J. W., Sack, G. C., Buckworth, R., & Manolis, C. S. (1983). An examination of *Crocodylus porosus* nests in two northern Australian freshwater swamps, with an analysis of embryo mortality. *Australian Wildlife Research*, 10, 571–605. <https://doi.org/10.1071/wr9830571>
- Webb, G. J. W., & Smith, A. M. A. (1984). Sex ratio and survivorship in the Australian freshwater crocodile *Crocodylus johnstoni*. *Symposia of the Zoological Society of London*, 52, 319–355.
- Webber, B.L., Yeoh, P.B., & Scott, J.K. (2014). *Invasive Passiflora foetida in the Kimberley and Pilbara: Understanding the threat and exploring solutions*. Phase 1 final report CSIRO, Australia.
- Whitaker, R., & Whitaker, Z. (1984). Reproductive biology of the mugger (*Crocodylus palustris*). *Journal of the Bombay Natural History Society*, 81, 297–317.
- Wilkinson, P. M. (1984). *Nesting ecology of the American alligator in coastal South Carolina*. SC Wildlife and Marine Resources Department, Division of Wildlife and Freshwater Fisheries.
- Wings, O. (2007). A review of gastrolith function with implications for fossil vertebrates and a revised classification. *Acta Palaeontologica Polonica*, 52, 1–16.
- Yangprapakorn, U., Cronin, E., & McNeely, J. (1971). Captive breeding of crocodiles in Thailand. *Crocodyles*, 32, 98–101.

**How to cite this article:** Somaweera R, Brien ML, Platt SG, Manolis C, Webber BL. Direct and indirect interactions with vegetation shape crocodylian ecology at multiple scales. *Freshw Biol.* 2018;00:1–12. <https://doi.org/10.1111/fwb.13221>