The ecological importance of crocodylians: towards evidence-based justification for their conservation

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ABSTRACT

Large-bodied predators are well represented among the world’s threatened and endangered species. A significant body of literature shows that in terrestrial and marine ecosystems large predators can play important roles in ecosystem structure and functioning. By contrast, the ecological roles and importance of large predators within freshwater ecosystems are poorly understood, constraining the design and implementation of optimal conservation strategies for freshwater ecosystems. Conservationists and environmentalists frequently promulgate ecological roles that crocodylians are assumed to fulfil, but often with limited evidence supporting those claims.

Here, we review the available information on the ecological importance of crocodylians, a widely distributed group of predominantly freshwater-dwelling, large-bodied predators. We synthesise information regarding the role of crocodylians under five criteria within the context of modern ecological concepts: as indicators of ecological health, as ecosystem engineers, apex predators, keystone species, and as contributors to nutrient and energy translocation across ecosystems. Some crocodylians play a role as indicators of ecosystem health, but this is largely untested across the order Crocodylia.

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By contrast, the role of crocodylian activities in ecosystem engineering is largely anecdotal, and information supporting their assumed role as apex predators is currently limited to only a few species. Whether crocodylians contribute significantly to nutrient and energy translocation through cross-ecosystem movements is unknown.

We conclude that most claims regarding the importance of crocodylians as apex predators, keystone species, ecosystem engineers, and as contributors to nutrient and energy translocation across ecosystems are mostly unsubstantiated speculation, drawn from anecdotal observations made during research carried out primarily for other purposes. There is a paucity of biological research targeted directly at: understanding population dynamics; trophic interactions within their ecological communities; and quantifying the short- and long-term ecological impacts of crocodylian population declines, extirpations, and recoveries. Conservation practices ideally need evidence-based planning, decision making and justification. Addressing the knowledge gaps identified here will be important for achieving effective conservation of crocodylians.

Key words: crocodile, alligator, apex predator, keystone species, ecosystem engineer, cross-ecosystem linkage, ecological indicator, freshwater ecosystem, conservation value

I. INTRODUCTION

Large-bodied predators, such as sharks, bears, wolves, big cats, and crocodiles, are among the most iconic animals on the planet, despite often being feared and reviled because of conflicts with humans and livestock (Treves & Karanth, 2003; Treves et al., 2004). These charismatic animals attract disproportionate amounts of research and conservation funding compared to other species. As a result, large predators (> 20 kg adult body mass) are one of the most intensively studied groups of animals (Sergio et al., 2006).

The importance of large-bodied predators for the stability, resilience, and functioning of terrestrial and marine ecosystems is well recognised (Heithaus et al., 2008a; Ritchie et al., 2012; Ripple et al., 2014). On land, significant cascading trophic interactions are controlled by the largest predators through either tri-trophic or mesopredator cascades (Ritchie et al., 2012; Ripple et al., 2014). In the world’s oceans, a decline in abundance of the largest predators, such as top-order sharks, has caused cascading impacts in marine communities, resulting in significant ecological damage (Heithaus et al., 2008a) and a demonstrated economic downturn (Myers et al., 2007). Large-bodied predators have far-reaching and underappreciated effects on myriad ecosystem functions and ecological processes, for example disease (Pongsiri et al., 2009), wildfire (Ripple et al., 2014), carbon sequestration (Duffy, 2003), impacts of invasive alien species (Wallach et al., 2010; Braczkowski et al., 2018), and biogeochemical processes (Schmitz, Hawlena & Trussell, 2010).

In sharp contrast, the roles of large-bodied predators in freshwater ecosystems remain poorly understood (Goymer, 2018; Hammerschlag et al., 2019). Studies on predator–community interactions within freshwater ecosystems have predominantly focused on small- to medium-bodied predators, such as invertebrates, fishes, and wading birds (Power, 1984; Carpenter & Kitchell, 1988; Estes et al., 2011). While fresh water makes up only 0.01% of the world’s water, and roughly 0.8% of the Earth’s surface, it supports some 6% (i.e. > 100,000) of all described species on Earth (Dudgeon et al., 2006). Freshwater ecosystems face increasing pressures from climate change, invasive alien species, anthropogenic disturbances, and many other factors (Ormerod et al., 2010; Pereira et al., 2010). They are considered by the Intergovernmental Panel on Climate Change (IPCC) to be among the most vulnerable ecosystems on the planet (Kundzewicz et al., 2008), yet there is limited understanding of the complex interactions that maintain their resilience (Lawler et al., 2006; Woodward, Perkins & Brown, 2010) and, in particular, the role that large-bodied predators play.
The largest inhabitants of many freshwater ecosystems are crocodylians. At least eight of 27 extant species reach more than 5 m in length and exceed 500 kg in body mass (Grigg & Kirshner, 2015). Even considering the large size variation within the Crocodylia (2.0–7.0 m maximum total body length), most species eclipse in size the largest freshwater predatory fishes (e.g. giant catfish, river sharks, and rays), carnivorous mammals (e.g. river dolphins, giant otters), and terrestrial predators that sometimes hunt in fresh waters (i.e. felids, ursids, and canids; Fig. 1). Amongst all aquatic predators, crocodylians are second in size only to the largest carnivorous cetaceans, pinnipeds, some sharks, and anadromous fish, such as sturgeon, paddlefish, and sawfish (Fig. 1). Members of the order Crocodylia are present in almost all types of freshwater habitats throughout the tropics, subtropics, and certain temperate regions (Edelman et al., 2014).

Fig. 1. Comparison of body size and mass of representative large vertebrate predators in the terrestrial, freshwater, and marine environments of the world. Silhouettes to scale based on the largest confirmed records: (1) polar bear Ursus maritimus; (2) kodiak bear Ursus arctos middendorffi; (3) Bengal tiger Panthera tigris; (4) African lion Panthera leo; (5) grey wolf Canis lupus; (6) giant river otter Pteronura brasiliensis; (7) green anaconda Eunectes murinus; (8) Wels catfish Silurus glanis; (9) Amazon river dolphin Inia geoffrensis; (10) estuarine crocodile Crocodylus porosus; (11) Chinese paddlefish Polyodon sinensis; (12) beluga sturgeon Huso huso; (13) great white shark Carcharodon carcharias; (14) sperm whale Physeter macrocephalus; (15) orca Orcinus orca; (16) southern elephant seal Mirounga leonina.
including lakes, ponds, rivers, creeks, swamps, marshes, flooded forests, man-made canals, and agricultural lands in around 100 countries (Groombridge, 1987; Martin, 2008). Moreover, several species also regularly occupy or forage intermittently within estuaries and near-shore marine habitats (Rosenblatt & Heithaus, 2011; Nifong & Silliman, 2017), and some make long-distance oceanic journeys (Read et al., 2007; Brackhane et al., 2018). This, and their dependence on terrestrial habitats for nesting make them the only aquatic predator group with extensive cross-ecosystem linkages.

Given their long evolutionary history (Buffetaut, 1979), there can be little doubt that crocodylians, and crocodyliiformes, have been influencing the evolution and ecology of other life forms and their physical environment for more than 200 million years. Yet, despite their large size and near-ubiquitous presence in freshwater ecosystems, an empirical understanding of their ecological importance is extremely limited. The ecological importance of a species encompasses all trophic interactions with other species, all non-consumptive direct and indirect contact with other species, and any activities that result in ecosystem modification (Heithaus et al., 2010). Although these predators interact with many members of their communities in diverse ways, we have limited understanding of the pathways, time scales, and effects of these interactions on ecosystem-level processes. Even so, statements assuming high ecological importance are common in the context of promoting and prioritising crocodile conservation efforts (Mceely & Sochaczewski, 1991).

References to their ecological significance are made commonly about almost all crocodylian species, especially in publications by government departments, conservation organisations, and scientific institutions (see online Supporting Information, Appendix S1). For example, the government of the State of Queensland in Australia affirms that protecting crocodiles is critical to keeping wetland environments healthy and stable (Queensland Government, 1995). The Wildlife Conservation Society of the Philippines claims that crocodiles are important for maintaining the balance of aquatic ecosystems by controlling population growth of prey species, maintaining residual waterholes during dry periods, and inhibiting encroachment of aquatic plants in these ecosystems (WCSP, 1997). Claims such as these are common, ecologically plausible and could well be true, but empirical evidence based on research is seldom provided, or available.

Whether these unsubstantiated assertions are justified is becoming increasingly relevant within crocodylian conservation and management programs. Conservation programs based on protection have been successful in many countries (Grigg & Kirshner, 2015), but not all. The increases in abundance of some crocodylians that results from protection has led to increased rates of human–crocodile conflict (Fukuda, Manolis & Appel, 2014; Brackhane et al., 2018, 2019), creating public and political demands for control measures (van der Ploeg et al., 2019). With commercially valuable species, protection has sometimes transitioned to ‘sustainable use’ initiatives, providing economic benefits for tolerating the increases in abundance and allowing wild populations to continue building (Webb, 2014). In others, unregulated harvesting for subsistence or other domestic uses and habitat loss remain problematic (Rödder et al., 2010; Thorbjarnarson & Wang, 2010; Stevenson, 2015). The IUCN Red List recognises seven species as meeting their criteria for Critically Endangered – 30.4% of the assessed species, worse than in any other taxonomic group (IUCN, 2017).

The ecological value of crocodylians is a potential driver of conservation action, which if successful, can provide ecological benefits. However, it is unclear whether the ecological roles crocodylians play are of sufficient magnitude that their demise will cause the sorts of ‘ecosystem collapse’ often suggested (Ashton, 2010; Ferreira & Pienaar, 2011). Referring to the widely believed ecological importance of the Critically Endangered Orinoco crocodile (Crocodylus intermedius) in Venezuela (via maintaining river courses through movements, controlling populations of piranhas, mediating ecological balance and productivity in the Llanos), Gorzula (1987, p. 96) argued that such claims should be regarded more as “myths than facts,” because none of the claims are supported by scientific evidence. Justification for the conservation of the Critically Endangered Philippine crocodile (C. mindorensis) is often based on assumptions about an important role they play in aquatic ecosystems (van der Ploeg et al., 2011b). Against such claims it could be argued that opportunistic field observations have not shown any detectable ecological change in wetland ecosystems after the severe historical depletion (<99% of biomass) of estuarine crocodiles (C. porosus) in the Northern Territory of Australia (Fukuda et al., 2011). Similarly, the zero-tolerance policy and removal of crocodiles in Darwin Harbour in northern Australia over the last 40 years (Fukuda et al., 2014) seems ecologically benign. However, only definitive ‘before and after’ experimental data would confirm these field observations.

Herein we review the literature about the ecological role of crocodylians, as a first step towards establishing a knowledge base regarding their ecological importance to the functioning of freshwater systems, as demonstrated for other large-bodied predators occupying terrestrial and marine ecosystems (Appendix S2; Fig. 2). Specifically, we examine five putatively ecological functions that might be ascribed to crocodylians: ecological indicators of ecosystem responses, ecosystem engineers, apex predators, keystone species, and mediators of cross-ecosystem linkages. We then review perceived or tangible anthropocentric values of crocodylians – economic, cultural, and intrinsic – because within different contexts, human actions relating to crocodylians are also influential in determining whether public support for conservation can be sustained. On the basis of knowledge gaps identified, we suggest priorities for future research on crocodylians and other large-bodied predators in freshwater ecosystems. In doing so, we aim to bring transparency and accountability to the ‘protect crocodylians for healthier ecosystems’ paradigm and, in place of unsubstantiated pseudo-ecological assertions, promote addressing knowledge shortfalls in order to establish an evidence-based process for justifying crocodylian conservation.

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II. CAN CROCODYLlANS BE USED AS AN INDICATOR OF ECOSYSTEM HEALTH?

Adaptive management provides a scientific framework that ultimately helps improve decision-making and management outcomes by reducing uncertainty through incorporating new information in response to unanticipated changes (Walters, 1986). Monitoring is a vital component of adaptive management (Busch & Trexler, 2002). Because it is rarely feasible to monitor everything in an ecosystem, researchers often select ecological indicator species as surrogates for ‘ecosystem health’ (Burkhard, Müller & Lill, 2008). The dynamics of this species can then be used to inform and guide a range of decision-making processes, including management and policy. However, claims that species are effective ecological indicators often exceed the empirical and experimental data they are based upon (Carignan & Villard, 2002). While the presence of any species can be said to indicate the set of specific ecological conditions required for their existence and persistence, at least in the short term, an effective ecological indicator species should: (i) be representative of the ecosystem; (ii) integrate system responses to change; (iii) show clear responses to management activities; (iv) be easier or cheaper to monitor than other response metrics (e.g. vegetation cover, water quality, etc.); and (i) be of management (conservation, production, or control) interest (Schiller et al., 2001; Doren, 2006; Doren et al., 2009; Mazzotti et al., 2009). For example, top-order shark abundance is considered an indicator of ecosystem health (Fulton, Smith & Punt, 2005), especially from a fisheries perspective (Arreguín-Sánchez, 2011; Espinoza et al., 2014), while bears have been used as indicator species in forest management and planning (Mitchell & Powell, 2003; Brodeur et al., 2008).

Several studies have documented the response of crocodylians to changes in environmental conditions, including changes in behaviour due to physiological and developmental impacts, focusing on habitat quality (Swanepeol, 1999), vegetation composition (Rosas et al., 2010), climate (Galván et al., 2012), and environmental contaminants (Guillette Jr et al., 1994; Wu et al., 2000b; Manolis, Webb & Britton, 2002; Campbell, 2003; Poletta et al., 2008) (Fig. 3). These studies span most species of crocodylians, a wide geographic range, and all ontogenetic stages (Appendix S1), suggesting there is strong potential for crocodylians to be used as effective indicators of ecological health. However, these studies were rarely directly tied to explicit hypotheses or experimental designs, and virtually never had pre-environmental change data available from which to develop models or make predictions, which limits inference from them to only tentative support for the idea that crocodylians may be useful indicator species for their ecosystems.

A prime example of the use of crocodylians as ecological indicators comes from the Florida Everglades, within the native range of two crocodylian populations, the American alligator (Alligator mississippiensis) and the American crocodile (C. acutus), both of which have recovered from historical over-harvesting. In this system, the direct relationships between biological-response metrics of resident crocodylians, such as abundance and body condition, and local hydrological conditions (Mazzotti & Brandt, 1994; Rice, Mazzotti & Brandt, 2005), have been used to track the progress of ecosystem restoration efforts (Mazzotti et al., 2009). In the case of the Everglades, the availability of well-established quantitative methods for monitoring restoration success (Mazzotti et al., 2003; Rice et al., 2007b) and multiple, robust, long- and short-term data sets has enabled the development of predictive models to assess impacts of water management (e.g. inundation and delivery of fresh water to estuaries) on indicator metrics established for resident crocodylians (Mazzotti & Brandt, 1995; Slone, Rice & Allen, 2003). For example, shortened periods of floodplain inundation result in diminished food resources, which results in fewer alligators and poorer body condition for those that remain (Waddle et al., 2013; Brandt et al., 2016). Researchers in the Florida Everglades continue to generate quantitative data (Waddle et al., 2015; Brandt et al., 2016), which are used to guide management (Brandt et al., 2014) and assist in developing targets to monitor restoration progress (Mazzotti et al., 2009; Brandt et al., 2016).

Overall, we conclude that the use of crocodylians as ecological indicators of ecosystem responses to management programs, or of ecosystem health in general, is still at an early stage with only a single system containing robust data. However, taken together, results from studies to date demonstrate that most crocodylians meet the criteria of ideal indicator species in that they represent integrated ecosystem change, show clear responses (e.g. reproductive output, body condition, abundance, etc.), can be monitored reasonably easily, and are often of central interest to management and conservation concerns. As threats to freshwater ecosystems persist and intensify in the future, and as more and more governments implement freshwater ecosystem protection, management, and restoration, opportunities to use crocodylians as ecological indicators and incorporate measurements of their ‘vital statistics’ into decision-making frameworks will likely expand.
III. ARE CROCODYLIANS ECOSYSTEM ENGINEERS?

Many organisms play a role in the creation, modification, and maintenance of the physical attributes of habitats in ways that influence the distribution, life histories, behaviours, and abundance of other species (Jones, Lawton & Shachak, 1994). Animals that undertake such activity are referred to as ecosystem engineers. While the activities of some herbivorous species, such as beavers, prairie dogs, deer, feral pigs, and elephants, result in significant physical changes to ecosystems [e.g. damming, changes to vegetation structure through grazing and browsing (Coggan, Hayward & Gibb, 2018)], hardly any other large-bodied predator directly manipulates their physical environment by as much as crocodylians (Fig. 4).

Crocodylians excavate open holes, dens, and tunnels as refuges from environmental extremes and predation, which also serve to store fresh water (Magnusson & Taylor, 1982; Martin, 2017). Mound-nesting species either build elevated structures in usually flat terrain (Campbell, 1972; Kushlan & Kushlan, 1980) or construct mound nests on floating vegetation (Hall & Johnson, 1987; Campos, 1993; Escobedo-Galván et al., 2011), consequently forming elevated ‘islands’.

While most crocodylians are solitary nesters, several species are known to nest in close proximity (predominantly driven by habitat availability), thus concentrating and amplifying habitat-modification effects across the landscape.

Fig. 3. Behaviours and interactions that exemplify crocodylians as ecological indicators. As long-lived aquatic predators, crocodylians could act as sentinel species to detect, monitor, and measure the impact of environmental contaminants and pollutants, including heavy metals, pesticides, herbicides, fossil fuels, and other harmful chemicals. In addition, researchers use the abundance, reproductive traits, and health of crocodylians as indicators of environmental conditions and ecosystem responses to management activities. Images left to right: in the Florida Everglades, the health and condition of American alligators (Alligator mississippiensis) are indicators of hydrologic conditions and resource abundance (photograph: M. Vieira). Examining the body condition of crocodylians requires morphometric measurements of individuals in the field, like these head measurements taken from a black caiman (Melanosuchus niger) in Guyana (photograph: J. C. Nifong). The physiology and condition of developing embryos can serve as indicators of environmental contaminants and are routinely used in scientific studies, like these American alligator eggs collected for analysis in Florida (photograph: J. C. Nifong). Crocodylians are hardy organisms, withstanding harsh physical conditions and typically recover quickly from sickness and injury; thus, poor body condition and possible disease, like in this American alligator (photograph: J. C. Nifong), could be indicative of a wider environmental concern.
[e.g. *A. mississippiensis* (Woodward et al., 1984), *C. acutus* (Thorbjarnarson, 2010), Nile crocodile *C. niloticus* (Cott, 1961), gharial *Gavialis gangeticus* (Rao & Singh, 1995)]. Furthermore, many species demonstrate a high degree of nest site fidelity, returning to specific nesting locations year after year. For mound-nesting species, this behaviour can promote the accumulation of nesting material and result in a greater degree of modification at specific locations (Vliet, 2001). With up to 50% of females constructing nests in any given year (Lance, 2003), the potential for large breeding populations of crocodylians to benefit other species is high.

Holes excavated by crocodylians can be more than 20 m in diameter, with depths greater than 1 m and surface areas spanning up to 1500 m² (Campbell & Mazzotti, 2004). Tunnels can reach over 50 m in length (Thorbjarnarson & Wang, 2010), and mound nests can reach 7 m in diameter and 1 m in height (Kushlan & Mazzotti, 1989). The regular use of pathways between key home-range features creates tracks and other depressions that can retain water in drier periods. Given the substantial size of habitat features and total area of physical modifications imposed by crocodylians, these activities have strong potential to influence topographic heterogeneity significantly within the landscape.

Physical structures constructed by crocodylians provide living, feeding, drinking, and breeding opportunities for a wide range of other animals. For example, holes created by alligators provide dry-season refuges for other aquatic organisms such as fish, aquatic invertebrates, reptiles, and amphibians when the surrounding marsh is periodically dry (Kushlan, 1974; Loftus & Eklund, 1994), and foraging sites for wading birds and mammals (Frederick & Spalding, 1994; Hoffman, Bancroft & Sawicki, 1994). Mounds created by alligators are used as raised nesting platforms by several species of reptiles (Kushlan & Kushlan, 1980; Elsey et al., 2013; Merchant, Murray & Cooper, 2014; Elsey et al., 2016), and as feeding sites by an array of birds and mammals (Merchant et al., 2014). Burrows dug by West African crocodiles (*C. suchus*) are often seasonally co-inhabited by many different insects, arachnids, amphibians, reptiles, and even bats, while burrows created and maintained by the dwarf crocodiles (*Osteolaemus spp.*), provide the only dry-season access to surface water in many forest habitats (M. H. Shirley, unpublished data).

However, whether these are largely facultative or obligatory interactions remains unknown, and the net impacts of these interactions have rarely been studied. In limited studies, shared nesting space with other animals was thought to be disadvantageous for crocodylians due to disturbance to nesting females (Dugan et al., 1981) and increased predation rates on eggs (Mazzotti et al., 2015). In a three-year study of the Florida red-bellied turtle (*Chrysemys nelson*), eggs were found in 20 of 103 American alligator nests examined (Kushlan & Kushlan, 1980), while another study found that a single alligator nest may hold up to 200 eggs of the northern red-bellied turtle *Chrysemys rubridorsis* (Deitz & Hines, 1980). A similar association has been observed between Amazonian yellow-spotted river turtles (*Podocnemis unifilis*) that nest in black caiman (*Melanosuchus niger*) nests (Maffei & Da Silveira, 2013). However, these studies did not evaluate the nesting effort of turtles at sites outside of alligator and caiman nesting locations; thus, the importance of alligatorid nests to the reproductive success of the turtle species is currently unknown. Additionally, the benefits provided by alligator holes as aquatic refugia varies both spatially and temporally because they are heterogeneously distributed, and only the deepest holes would have any value as aquatic refugia during the driest years (Mazzotti & Brandt, 1994).

Nevertheless, at a local scale all these structures may contribute more to the ecosystems in which they are found than so far realised. Removal of vegetation and alteration of soil properties through movement of soil allows for changes in plant community composition and structure that may be physically, chemically, and biologically distinct from the surrounding undisturbed marsh, allowing plant species with different habitat requirements to establish in flooded habitats (Campbell & Mazzotti, 2004; Palmer & Mazzotti, 2004). Abandoned nest mounds contribute to the formation of tree islands in wetland habitats (Craighead, 1969). In a comparative study, Palmer & Mazzotti (2004) demonstrated that alligator holes enhance spatial heterogeneity and influence plant community composition and structure through increased biodiversity.

Preliminary evidence suggests that crocodylian populations do have the potential to exert effects on the environments they inhabit and the population dynamics of other species that take advantage of habitat features engineered by crocodylians. Empirical evidence of noteworthy benefits to other animals *via* crocodylian ecosystem engineering exists to date for only one species—the American alligator—through its creation of seasonal refuges and novel living and foraging opportunities for plants and animals. Other crocodylian species physically alter their environments in comparable ways and, therefore, may indeed have significant ecosystem engineering roles, particularly in relation to plant communities and the creation of microhabitat, but the lack of large-scale and/or long-term studies on most species hinders evidence-based conclusions.

IV. ARE CROCODYLIANS APEX PREDATORS REGULATING POPULATIONS OF THEIR PREY?

A significant ecological role of large-bodied carnivores in general is implied by their being grouped as apex predators (Ordiz, Bischof & Swenson, 2013; Wallach et al., 2015). They consume many prey over a lifetime, thereby influencing populations of other animals, and are rarely eaten themselves after reaching adult size (Sergio et al., 2014). Crocodylians are commonly categorised as apex predators because they are assumed to have a significant influence on the populations of their prey and are considered invulnerable as adults (Fig. 5). Validation of this as a suitable categorisation, however, is problematic for three reasons.
First, determination of the complete diet of crocodylians is difficult (Rosenblatt et al., 2015). Their cryptic, nocturnal, infrequent, and aquatic hunting behaviours make field observations of feeding extremely difficult (Nifong et al., 2014). Interpretation of stomach-content data is hindered by differential digestion rates within and among prey species (Davenport et al., 1990; Balaguera-Reina et al., 2018), accumulation of indigestible prey parts (Nifong et al., 2012), and possible secondary ingestion of non-target prey (Jackson, Campbell & Campbell, 1974; Taylor, 1979). Where these factors were controlled, the estimated rates of feeding and the relative contributions of different prey items were markedly different from where they were not controlled (Webb, Hollis & Manolis, 1991). Crocodylian diets vary strongly across space and time (Rosenblatt & Nifong, 2018; Santos et al., 2018), making overall dietary extrapolations from snapshot stomach content samples difficult. For example, field observations, as well as stable isotope data (Radloff, Hobson & Leslie, 2012), suggest that large herbivores could be a substantial component of the diet of large Nile crocodiles during the peak dry season, when terrestrial herbivores attracted to dwindling water sources provide seasonal predation (Subalusky et al., 2017) and scavenging (Radloff et al., 2012) opportunities. Even smaller species of crocodylians will consume large prey when food is scarce, typically during dry seasons (Thorbjarnarson, 1993; Somaweera et al., 2018b). However, obtaining stomach samples non-lethally from large crocodylians is logistically difficult and seldom attempted (Wallace & Leslie, 2008), and stable isotopes are not appropriate to determine trophic position.

**Fig. 4.** Behaviours and interactions that exemplify crocodylians as ecosystem engineers. Many crocodylians construct and maintain a variety of habitat features, including shallow depressions, open holes, ponds, burrows, tunnels, and dens. These features benefit other species by providing refuge, prey, and fresh water, and can establish unique environmental conditions. Images left to right: many crocodylians excavate shallow ponds and build large mound nests, such as this American alligator (*Alligator mississippiensis*) nest and nursery pond in Louisiana (photograph: R. Elsey). Crocodylian nests and surrounding areas serve as oviposition sites for several reptile species, like these skink eggs found within an American alligator nest cavity (photograph: R. Elsey). Crocodylians construct above-ground nests by mounding vegetation and soil; nests can be large, reaching 7 m in diameter × 1 m in height, like this American alligator nest (photograph: J. Nifong). In addition to nursery ponds and nests, certain crocodylians excavate and maintain complex burrows and dens like these dug by Nile crocodiles (*Crocodylus niloticus*) (photograph: A. Kilpin). These burrows are used as refuges from harsh conditions or predation by multiple species of animals, including smaller crocodylians.
of crocodylians (Villamarín et al., 2018), resulting in a paucity of reliable data on complete dietary profiles of larger size classes of crocodylians. Second, crocodylians are able to survive on significantly smaller amounts of food relative to their body mass than are large endothermic predators (Magnusson & Lima, 1991; Grady et al., 2019). Crocodylians feed more frequently and grow faster within the first years of life. From a fitness perspective, this is advantageous because, as they grow, they become increasingly less vulnerable to a wide range of potential predators, including larger crocodylians (Somaweera, Brien & Shine, 2013). However, feeding frequency and growth rate generally declines with increasing body size, as evidenced by the proportion of crocodiles with either empty or near-empty stomachs at any one time increasing with body size (Cott, 1961; Taylor, 1979; Grigg & Kirshner, 2015), although some studies show otherwise (e.g. Balaguera-Reina et al., 2018). As with most ectotherms, crocodylians are highly efficient at converting food to energy (Grigg & Kirshner, 2015). For example, juvenile estuarine crocodiles in the wild are known to consume the food equivalent of only ~4% body mass per week and with a conversion efficiency (i.e. wet mass prey converted to wet mass crocodile) as high as 82.4% (Webb et al., 1991). Different size classes of many crocodile species in the wild are capable of going without food for many months during extreme extended dry seasons (Shine et al., 2001; Brito et al., 2011) or periods of drought (Hayesodum & Jones, 1993). Some wild-caught male estuarine crocodiles placed in captivity are known to have survived for up to 12 months without food, relying on body fat stores.

Last, as ectotherms, crocodylians are strongly influenced by their thermal environment, exhibiting reduced activity, frequency of feeding, and rates of digestion as temperatures decrease (Webb, Manolis & Buckworth, 1982; Hutton, 1987; Wallace & Leslie, 2008). Some species of crocodilian will cease feeding altogether during winter, when ambient temperature drop below the threshold minimum required for digestion (Lang, 1987), or enter aestivation during extreme dry seasons (Shine et al., 2001; Brito et al., 2011; Campos & Magnusson, 2013). Aestivation can last anywhere from several weeks to several months depending on the location, with individuals needing less energy and relying on body fat stores.

Over geological time crocodyliiforms have had varied diets (Melstrom & Irmi, 2019), but massive species such as Sarcosuchus (total length approximately 11 m) likely preyed on large adult dinosaurs, placing them in terminal positions in the food web (Farlow & Holtz, 2002). All extant crocodylians are obligate carnivores and need to consume animal prey to maintain homeostasis, grow, and reproduce (Staton et al., 1990). However, an empirical assessment of trophic position, like those for other predators (Crawford et al., 1992; Cortés, 1999), is unavailable for crocodylians (Villamarín et al., 2018). Studies of trophically transmitted crocodylian parasites are beginning to reveal cryptic data about trophic links (Tellez & Nifong, 2014; Tellez & Sung, 2018), but so far these data are available only for the American alligator. An emerging body of literature demonstrates that while adult crocodylians do consume large vertebrates, including other predators as prey (and carrion), a significant portion of their diet comprises invertebrates and smaller-bodied vertebrates, many residing in low trophic levels (Cott, 1961; Diefenbach, 1979; Waitkuit, 1986; Ouboter, 1996; Luiselli, Akani & Capizzi, 1999; Riley & Huchzermeyer, 2000; Pauwels, Barr & Sanchez, 2007; Rice et al., 2007a; Bortiero et al., 2009; Platt et al., 2013; Rosenblatt et al., 2015; CRISPS, 2017; Shirley et al., 2017). To complicate the matter further, estimates of trophic position for crocodylians based on stomach-content analyses regularly conflict with interpretations of trophic position based on stable-isotope analysis (i.e. δ15N: Villamarín et al., 2018).

As opportunistic, generalist predators, the prey types of crocodylians usually reflect what is available in the environment, and this clearly changes seasonally, over short time periods, and even from population to population (Grigg & Kirshner, 2015). Many prey species, such as migrating wildebeest (Pooley, 1989) or nesting waders (Caut et al., 2019), interact with crocodylians for only a short period of the year. Some prey, such as bats, may be a very important and sustainable food source for a small number of populations of any particular crocodylian species, but are taken less frequently and opportunistically by many others (Shirley et al., 2017). The susceptibility of prey also depends on habitat conditions, and the principle prey taken in some habitats in a given season may vary among years (Santos et al., 1996). Seasonal variation in crocodylian habitats certainly results in highly seasonally variable food intake – for example, dry season concentrations of crocodylians and prey into confined habitat may result in considerable seasonal impacts on prey populations (Whitfield & Blaber, 1979).

Overall, there is a lack of methods and insight that allow us to define how crocodylians impact prey populations. Even so, there is limited information to support the argument that crocodylians are apex predators controlling populations of prey, either year round or seasonally. Furthermore, despite concentrated feeding events, crocodylians generally feed infrequently, consume a small amount of food on average relative to body size, and have periods of the year when feeding may cease altogether in some species. Taken together, the available evidence suggests that crocodylians do not appear to conform to the traditional concept of an apex predator.

V. ARE CROCODYLIANS KEYSTONE SPECIES CAUSING CASCADING IMPACTS?

Numerous experimental studies manipulating the presence and abundance of large-bodied predators have demonstrated profound effects on community structure and ecosystem functioning in terrestrial and marine environments (Fortin et al., 2005; Myers et al., 2007; Levi & Wilmer, 2012; Ordiz et al., 2013). The loss of the largest predators...
can disproportionately disrupt ecosystem structure and function (Ripple et al., 2014), a process termed ‘trophic downgrading’ (Estes et al., 2011). Large-bodied predators can play a key role in ecosystems by regulating the abundance and behaviour of smaller predators (i.e. mesopredators) and other lower-order consumers (Prugh et al., 2009; Estes et al., 2011). The loss of large-bodied predators removes this inhibiting factor, resulting in ‘mesopredator release’ (Crooks & Soulé, 1999; Ritchie & Johnson, 2009), causing direct and indirect cascading impacts within the ecosystem, termed ‘trophic cascades’. Such cascades are well documented for the marine realm from changes in shark abundance (Myers et al., 2007; Ferretti et al., 2010; Barley, Meekan & Meeuwis, 2017) and in the terrestrial realm from changes in canid abundance (Ripple & Beschta, 2004; Glen et al., 2007; Beschta & Ripple, 2009).

Popular literature often cites crocodylians as keystone species, defined here as those that have far-reaching impacts on the ecosystems they occupy, to the extent that cascading effects will occur if they are removed. Apart from the broad usage of the terminology, as well as the technical and theoretical limitations surrounding the keystone species concept (Power et al., 1996; Soulé et al., 2005; Cottee-Jones & Whittaker, 2012), there is uncertainty about whether crocodylians play a key role in any ecosystem. As predators, crocodylians can reach extraordinarily high densities, either generally or during seasonal aggregations, so their impact on food webs could be high. This was probably historically true for most crocodylian species (e.g. Audubon, 1827; Bartram, 1980) and is still true today for some populations of some species (Mourão et al., 2000), that form highly concentrated aggregations when water bodies are limited in dry seasons (Webb, Manolis & Buckworth, 1983).

Effects of crocodylians on prey proceed through two pathways: (i) consumptive effects (i.e. through capturing, killing, and consuming prey), and (ii) non-consumptive effects (i.e. causing changes in prey behaviour, growth, or morphology due to the presence of a predator) (Fig. 5). Consumptive effects are comparatively easy to detect, but only a single study to date has experimentally investigated the effects of exclusion of a crocodylian on prey. Martin & Hight (1977) demonstrated that apple snails (Pomacea paludosa) increase in abundance in the absence of alligators. In the only well-documented study examining potential non-consumptive effects of crocodylians, Nifong & Silliman (2013) experimentally demonstrated within a controlled environment that American alligators can reduce the abundance (consumptive effect) and modify the behaviour (non-consumptive effect) of blue crabs (Callinectes sapidus), an important mesopredator in saltmarsh food webs, resulting in increased survival of both a keystone grazer (periwinkle snails Littoraria irrora) and an important mutualist of the grazer (ribbed mussels Geukensia demissa). These findings demonstrate that American alligators have the potential to generate trophic cascades within saltmarsh habitats.

Several field studies hypothesised that crocodylian nest-protection behaviour benefits other species that nest close to crocodylian nests [e.g. birds (Robinson, 1985; Post & Seals, 1991; Haemig, 2001; Burner, 2011; Nell, 2014), reptiles (Deitz & Jackson, 1979; Kushlan & Kushlan, 1980; Hall & Meier, 1993)], but none provides empirical support for their claims (e.g. through demonstrated increases in nest or hatching survivorship from these associations). Other studies have shown that visits to wading bird nesting sites by terrestrial predators are not hindered by the presence of crocodylians (Frederick & Collowy, 1989).

Crocodylians are also considered to have a keystone ecosystem function by controlling invasive alien species. For example, using population modelling, Keddy et al. (2009) concluded that American alligators have the potential to control the abundance of introduced nutria (Myocastor coypus) in the marshes of Louisiana, USA, and could help to mitigate the negative impacts of nutria on marsh vegetation and other processes. While nutria is a common food item of alligators (Gabrey, Kinker & Elsey, 2009), there is no experimental confirmation of this hypothesis.

The most commonly discussed effect of crocodylians on aquatic food webs is through their impact on fish abundance, a resource also harvested by humans. Several anecdotal observations relate increased fish yield in commercial catch to the presence of crocodylians and decreased fish yields to the demise of crocodylians. McNeely & Sochaczewski (1991, p. 205), for example, asserted “Studies have shown that the presence of crocodylians in a river actually increases the yield of fish…Crocodylians eat ailing fish in a significantly higher proportion than healthy fish, thus improving the common health of the fish stock…” Cott (1961) claimed that the presence of Nile crocodiles may keep predatory and ‘unwanted cannibal fish’ and spot-necked otter (Lutra maculicollis) numbers low, therefore benefitting fisheries. Nile crocodiles were also thought to feed extensively upon the commercially non-valuation African sharptooth catfish (Clarias mossambicus) at Mweru Wa Ntipa, but not tilapia (Tilapia sp.), a common commercial fish (Cott, 1961). Indigenous communities in India, Belize, and Cambodia use the presence of crocodylians as an indicator of good fishing (Whitaker & Whitaker, 1989; M. Tellez & S. G. Platt, personal observations). The decline and disappearance of crocodylians, therefore, has been attributed to declines in fishery stocks and the degradation of ecosystems through cascading ecological effects.

However, this argument is not yet supported by empirical data, and relationships likely represent correlation rather than causation. The studies proposing a link between crocodylian numbers and fish abundance fail to differentiate between the factors responsible for the decline of crocodylians and those that caused declines in other aquatic fauna, including fish. For example, freshwater wetland ecosystems in the Philippines have undergone unprecedented changes over the past century, caused by overharvesting, pollution, invasive species and habitat loss – not by declining populations of Philippine crocodiles (van der Ploeg et al., 2011a).

From a theoretical perspective, ecosystem models suggest that crocodylians could be expected to act as keystone species through their strong effects on prey in some ecosystems (Fittkau, 1970; Bondavalli & Ulanowicz, 1999; Silliman, 2011).
Grosholz & Bertness, 2009), but not in others (Villanueva, Ouedraogo & Moreau, 2006). Beyond the study by Nifong & Silliman (2013), we found no empirical studies that actually assessed whether or not crocodylians operate as keystone species. Although increased crocodylian abundance has been used as a measure of the success of ecosystem restoration efforts (Mazzotti et al., 2007), there is as yet no investigation into whether increasing numbers of crocodylians results in restoration of ecosystems or benefits to lower trophic levels.

Thus, we conclude that while crocodylians do elicit consumptive and non-consumptive effects on their prey, and that these effects have the potential to cascade through simplistic food webs, there is as yet no compelling evidence that it occurs. By contrast, research in terrestrial and marine ecosystems generally supports the view that the loss of large-bodied predators has clear impacts on food web structure and even ecosystem functioning (Fortin et al., 2005; Levi & Wilmer, 2012; Canning & Death, 2017). We found there is insufficient information and research to confirm or refute claims that crocodylians are keystone species and that their loss results in cascading impacts.

VI. DO CROCODYLIANS MEDIATE CROSS-ECOSYSTEM LINKAGES AND NUTRIENT FLUXES?

Oligotrophic (nutrient poor, low productivity) ecosystems can be functionally connected to other ecosystems through

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Fig. 5. Behaviours and interactions that exemplify crocodylians as apex predators and keystone species. Crocodylians consume a wide range of prey, from small invertebrates to large mammals and even other crocodylians. Moreover, the ecological roles of crocodylians can go beyond direct impacts on their prey to include indirect or cascading effects that are potentially important mechanisms whereby crocodylians can influence community and ecosystem structure and functioning. Images left to right: in salt marshes, American alligators (Alligator mississippiensis) have the potential to elicit trophic cascades through their consumptive and non-consumptive interactions with an important mesopredator, the blue crab (Callinectes sapidus) (photograph: T. J. Dunkerton). In Louisiana marshes, American alligators readily consume prey from lower trophic levels such as apple snails, an important grazer in the ecosystem, as evident from this alligator stomach containing numerous snail opercula (photograph: R. Elsey). Crocodylians do take large prey occasionally, sometimes when their usual food is scarce, like this Australian freshwater crocodile (Crocodylus johnstoni), a small-fish eating species, taking a large freshwater sawfish during the peak dry season in the Kimberley (photograph: WA Department of Biodiversity Conservation and Attractions), or when large prey are seasonally abundant, like these Nile crocodiles (Crocodylus niloticus) preying on zebras during the migratory period in Kenya (photograph: M. Kirubi).
animal movements that transfer energy, matter, or organisms across ecosystem boundaries (Watts & Handley, 2010; Mitchell, Bennett & Gonzalez, 2013). These movements frequently cause influxes of resources from areas of high productivity to those of low productivity (Shepard et al., 2013) and can also lead to increased ecosystem complexity and promote food web stability (Schreiber & Rudolf, 2008). Such linkages and fluxes caused by large-bodied predators are rare in terrestrial and marine ecosystems (Polis, Anderson & Holt, 1997; Schnitz et al., 2010; Bartels et al., 2012).

As amphibious large-bodied predators, crocodylians are unique in this sense. Over their lifetime, most crocodylian species travel between multiple habitats within freshwater, terrestrial, marine, brackish, and even into caves and other subterranean environments (Campbell et al., 2010a; Somaweera, Woods & Sonnenman, 2014; Shirley et al., 2017), inevitably acting as biological vectors of connectivity between otherwise disparate ecosystems. Telemetry studies on several crocodylian species demonstrate these cross-ecosystem travels, which include movement of adults between habitats for feeding and reproduction, or movements of different life stages due to ontogenetic shifts in habitat and prey use (Rosenblatt & Heithaus, 2011; Campbell et al., 2013; Nifong, Layman & Silliman, 2015) (Fig. 6). Moreover, all crocodylians nest and

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**Fig. 6.** Behaviours and interactions that exemplify crocodylians as mediators of cross-ecosystem fluxes and functional linkages. Left panel shows cross-ecosystem linkages established by the movement of crocodylians between and among disparate ecosystems. Several species of crocodylians repeatedly move between different aquatic habitats (freshwater, brackish, and marine) likely to exploit food resources. All species of crocodylians move between aquatic and terrestrial habitats for nesting, and through ontogeny (some more than others) for feeding. Images left to right: multiple species of crocodylians perform repeated movements between marine and freshwater ecosystems, like this American alligator (*Alligator mississippiensis*) exploring the sea floor off the Atlantic coast of Florida (photograph: L. Ruda). All crocodylians lay eggs on land (like this Australian freshwater crocodile (*Crocodylus johnstoni*) in Kimberley; photograph: R. Somaweera), and most species guard their nests throughout the incubation period during which they regularly move nutrients from aquatic systems to terrestrial systems via excretion. Right panel depicts cross-ecosystem linkages established through trophic interactions. All life stages of crocodylians are vulnerable to terrestrial predators, thus transferring energy and nutrients derived from aquatic systems to the surrounding terrestrial ecosystem. Likewise, throughout all life stages most crocodylians consume terrestrial prey, thus transferring energy and nutrients derived from terrestrial systems into aquatic ecosystems. Images left to right: while it is rare, even large crocodylians fall prey to big cats like this leopard (*Panthera pardus*) hunting a Nile crocodile (*Crocodylus niloticus*) at Kruger NP (photograph: H. Brindley). Through all life stages, crocodylians consume terrestrial species, ranging from small insects to larger terrestrial mammals like this Indian pangolin (*Manis crassicaudata*) consumed by a mugger crocodile (*Crocodylus palustris*) in Sri Lanka (photograph: J. M. Probst).
deposit eggs in terrestrial ecosystems. With high rates of nest failure due to environmental conditions and predation, much of the biomass and nutrients contained in crocodylian eggs eventually enters terrestrial food webs.

Foraging behaviours across ecosystems by crocodylians could facilitate the transfer of nutrients derived from one ecosystem to another (Subalusky, Fitzgerald & Smith, 2009), but this has yet to be clearly demonstrated. Recent studies on American alligators (Rosenblatt & Heithaus, 2011; Rosenblatt et al., 2013a; Nilong & Silliman, 2017), estuarine crocodiles (Kay, 2004; Hanson et al., 2015; Adame et al., 2018), and Amazonian crocodylians (Villamarín et al., 2017) using telemetry, stomach contents, and stable isotope analyses have demonstrated that travel between different environments, and the consumption of prey from distinct food webs, serve functionally to link discrete ecosystems. These movements may be along river systems (Crespo et al., 2015), between temporary and permanent water bodies (Grant et al., 2008), and between aquatic and terrestrial systems (Paolillo & Gorzula, 1993).

Based on anecdotal observations and information from local residents, Fitzkau (1970) postulated that caimans transfer nutrients essential for primary production by feeding in the nutrient-rich main channel of the Amazon River and defaecating in nutrient-poor tributaries. He associated declines in fish populations in these tributaries to a lack of productivity caused by over-hunting of caiman populations. He later asserted that caiman can theoretically add nutrients of allochthonous origin in quantities that are sufficient to enable an elevation in primary productivity in these habitats (Fitzkau, 1973). However, these findings remain speculative and controversial (Magnusson, 1990).

Crocodylians of all sizes and life stages could link aquatic and terrestrial habitats trophically by consuming prey from terrestrial habitats (Sah & Stuebing, 1996; Hanson et al., 2015; Nell & Frederick, 2015; Pringle, 2017; Adame et al., 2018) and by being prey of predators in terrestrial habitats (Shine, 2011; Somaweera et al., 2013; de Miranda, 2017). They may also functionally connect lentic and lotic habitats by movements across landscapes (Subalusky et al., 2009), and even connect surface and subsurface habitats through extensive burrow networks. There are empirical studies reporting increased productivity as a result of nutrient fluxes across landscapes in other systems, such as from above ground to subterranean environments by bats (Gnasini & Trajano, 2000), from water to land by seabirds (Anderson & Polis, 1999), and from oceans to rivers by salmon (Jonsson & Jonsson, 2003). Although crocodylians functionally connect disparate habitats, no studies have yet estimated the amount of resources translocated and their significance to recipient ecosystems.

VII. MOVING FORWARD: GAPS AND ALTERED APPROACH

Our survey of the available literature found that relatively few studies exist that assess empirically the ecological importance of crocodylians. There seem to be no studies that document notable changes in ecosystem status in places where crocodylians have been seriously depleted, even to the brink of extinction, or have subsequently recovered (Oum et al., 2009). This perhaps reflects in part the historical decline in most crocodylian populations when documenting the ecological impacts was not a research priority. In locations where crocodylian populations are now rebounding, the lack of ‘before’ data confounds objective comparison. An understanding of the ecological role of crocodylians as mesocarnivores, and their impacts on food webs and ecosystem function, will require a significant new research effort. Similarly, anecdotal evidence for crocodylians having a role as gene transporters, by hosting barnacles, rotifers, and epibions (Monroe & Garrett, 1979; Magnusson, 1985; Cupul-Magaña et al., 2011), and in reducing the spread of disease by scavenging (Subalusky et al., 2017), requires further research. That crocodylians in general may have utility as indicator species of ecosystem health and function (Ray et al., 2013), could be a positive force for their conservation, but this requires more research with different species in different ecological contexts.

Arguably, every species affects others in its ecosystem to some degree. Impacts on interactions that result from removing crocodylians, or allowing them to recover, could theoretically take multiple generations to manifest (van de Koppel et al., 2015). Direct and indirect effects may be difficult to attribute to the loss or recovery of crocodylian species due to the multitude of potential pathways through which impacts can occur (Ritchie & Johnson, 2009), especially in light of concurrent or on-going impacts from other forms of freshwater habitat modification (Davidson, 2014) and freshwater resource overexploitation (e.g. Allan et al., 2005). Our (in)ability to identify resulting impacts of changes in crocodylian presence and abundance requires a clearer, process-based understanding that includes spatial and temporal context (Ritchie et al., 2012). Informing conservation management through this improved ecological understanding will no doubt remain important. However, equally we need to balance this insight with other value propositions for identifying the importance of crocodylians in prioritising management outcomes (Table 1).

VIII. PROPOSED FUTURE RESEARCH

A fundamental problem with our understanding of crocodylians and their ecological importance to aquatic ecosystems is that most claims of ecological benefit stem from studies undertaken primarily for other purposes. The ecological roles proposed constitute speculative hypotheses, rather than conclusions based on evidence. Such speculation may help rationalise incentives for conservation, even if it is not evidence-based, but it creates an ethical dilemma for some scientists. Without strong empirical data upon which to base ecological justifications for conservation, scientists and other
Table 1. Crocodylians as tools for conservation

<table>
<thead>
<tr>
<th>Tool category</th>
<th>How crocodylians are used</th>
<th>Crocodylian example</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conservation symbols</td>
<td>Use crocodylians as icons, emblems, or symbols for conservation initiatives to harness public support for biodiversity conservation</td>
<td>Philippine crocodile (<em>Crocodylus mindorensis</em>) is used as an icon to boost pride among the community, respect for nature, and interest in wildlife among people in Luzon (Philippines) (van der Ploeg et al., 2011b)</td>
</tr>
<tr>
<td>Conservation of priority areas</td>
<td>Presence of rare and threatened crocodylians informs placement of priority conservation areas to conserve biodiversity</td>
<td>Gharial (<em>Gavialis gangeticus</em>) conservation efforts at National Chambal Sanctuary in India benefits numerous other species in the river system  (Nair &amp; Krishna, 2013; Sharma &amp; Singh, 2015; Singh &amp; Rao, 2017)</td>
</tr>
<tr>
<td>Monitoring the status of biodiversity</td>
<td>Routine evaluation of crocodile presence or population status used as a proxy for monitoring erosion of biodiversity, ecological integrity, or status of biodiversity</td>
<td>Gharial numbers used as an indicator of the health of the Ganga river ecosystem in India  (Behera, Singh &amp; Sagar, 2014), and American alligators (<em>Alligator mississippiensis</em>) in the Everglades restoration project  (Cherkiss et al., 2006)</td>
</tr>
<tr>
<td>Generation of revenues and income</td>
<td>Presence of crocodylians for consumptive and non-consumptive commercial use provides incentive to maintain natural state of ecosystems and preserve other elements of biodiversity</td>
<td>Harvesting common caiman (<em>Caiman crocodilus</em>) in large ranches in Venezuela is a basis for effective wildlife conservation and sustainable wildlife use  (Hoogesteijn &amp; Chapman, 1997)</td>
</tr>
</tbody>
</table>

conservation-minded people are limited to highlighting the non-ecological but tangible values of crocodylians to society – economic, cultural, or intrinsic – to incentivise and sustain conservation action (Appendix S3).

The high uncertainty around the conclusions reached throughout this review reflects the lack of targeted and directed research into questions pertaining to ecological value. To achieve a clear, process-based understanding of the ecological importance of crocodylians, we urge the crocodile ecology and conservation community to implement question- or hypothesis-driven research linking crocodilian abundance and behaviour to trophic interactions, environmental stability, and ecosystem resilience. We propose three key areas where further research could generate evidence-based insights into the ecological role of crocodylians in freshwater ecosystems.

(1) Population dynamics. Emerging techniques in remote monitoring of animals, long-term movement tracking, mechanistic models, and big data approaches are improving the ability to generate a mechanistic understanding of crocodylian population dynamics, including population growth and decline, demographic change, and resilience to global environmental change threats, including climate change, invasive alien species, and land-use change.

(2) Trophic interactions. Recent advances in stable isotope, fatty acid, and genetic analysis methodologies could play a crucial role in studying the trophic interactions of crocodylians, including how they exert regulatory influences within trophic systems through predation and habitat creation, and how they bridge terrestrial–aquatic ecosystem divides. Extending these investigations to predict how climate change-driven disruption in hydrological regimes may affect ecosystem stability and how overexploitation of some freshwater aquatic resources may compete with others, including large-bodied freshwater predators, will facilitate implementation of evidence-based conservation actions.

(3) Impacts of decline and extirpation. Investigations into long-term impacts of the decline or extirpation of crocodylian populations are needed to evaluate the possibility of ‘resetting ecosystems’ and predicting their susceptibility to further perturbations. Both ‘natural’ experiments (e.g. before-and-after studies where population abundance is changing) and controlled experiments (e.g. enclosure and exclusion experiments, managed harvest, removal or reintroduction studies) are both likely to be fruitful avenues. Within this scope, capitalising on crocodile harvest (i.e. restricting take based on size or sex, or having specific areas off-limits to harvest) or head-start and/or reintroduction programs, might provide cost-effective ways to establish experimental treatments.

Earth is presently in the midst of its sixth mass extinction event (Wake & Vredenburg, 2008), which is likely to impact extant large-bodied predators strongly (Ray et al., 2005). Numerous stressors caused by human activities across all ecosystems are threatening the existence and persistence of large-bodied predators. Given the central role that large predators are considered to play in ecosystems, this ‘trophic downgrading’ has generated widespread concern (Stier et al., 2016). However, despite their disproportionate relative contribution to ecosystem structure and function, our understanding of the functioning of freshwater ecosystems and the large predators that call them home, is in its infancy.
Crocodylians appear to have weathered conservation threats reasonably well so far. Species hunted almost to extinction have demonstrated a remarkable capacity to recover if habitats are intact and well-planned conservation programs, supported by legislation and funding, are in place. Yet threats ranging from habitat change to unregulated subsistence and commercial harvest, and human–crocodile conflicts, still mean that half of the world’s crocodylian species meet the IUCN criteria for being threatened with extinction – that is, Vulnerable, Endangered, or Critically Endangered on the IUCN Red List (IUCN, 2017; Appendix S1). Incentivising conservation action remains a challenge. Moreover, in addition to those known threats already discussed, ongoing climate change (Gibbon et al., 2000) and the impact of invasive alien species (Leslie & Spotila, 2001; Somaweera et al., 2012; Somaweera et al., 2018a, 2019) could both threaten the stability and resilience of crocodylian populations in ways as yet unknown.

Irrespective of the true ecological value of crocodylians, that there is a clear moral imperative to conserve crocodiles, for their intrinsic value alone, is appreciated by some but not others. Yet scientists, land managers and policy makers around the world frequently promote ecological reasons to justify crocodylian conservation. As we have shown here, the body of literature supporting these claims is limited. Many knowledge gaps remain in our understanding of the ecological importance of crocodylians, and the scale and pathways through which they could influence the stability and functionality of the world’s aquatic ecosystems. That every species in an ecosystem, including crocodylians, has a role in ecological structure and function is not in question. But overstating that role to the public, in the absence of supporting evidence, undermines the critically important contribution science and scientists make to evidence-based conservation actions.

Future crocodylian management, irrespective of what further research finds, will most likely require both conservation and control of “problem crocodiles” based on local context and a range of social, economic and environmental priorities. We caution that there are inherent risks associated with passing off untested assumptions as though they were facts. For example, making decisions on either the conservation or control of crocodylians based on weak evidence or mere assumptions could lead to serious consequences and cascading impacts that ultimately erode public support for crocodylian conservation. An evidence-based approach is needed to replace the uncertainty and speculation that is too often replacing more robust questions about the functional gain of crocodylian populations.

IX. CONCLUSIONS

(1) Compared to large-bodied predators in the terrestrial and marine realms, the roles and relative importance of large predators in freshwater systems are poorly understood.

(2) Scientists and other conservation-minded people often try to counter the desire to control or eradicate crocodylians by promoting their assumed ecological importance. However, our survey of the literature has shown that knowledge concerning significant ecological roles is sparse, and that targeted research on this fundamental issue is lacking.

(3) For most species, the usefulness of crocodylians as ecological indicators within coordinated management programs is unclear; their influence on ecosystem engineering is largely anecdotal; and their assumed role as apex predators regulating prey populations, generating trophic cascades, and influencing cross-ecosystem linkages is largely untested.

(4) Interacting forces degrading crocodylian populations, habitats, and prey populations over time make it difficult to tease apart these effects and identify correlation versus causation.

(5) Reliable assessments of population dynamics, trophic interactions, and evaluation of the long-term impacts of natural or experimental crocodylian declines, extirpations, or recoveries conducted within an explicit, question- or hypothesis-driven research framework will be important to moving beyond past anecdotes to evidence-based inferences on the ecological roles of crocodylians.

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XI. AUTHOR CONTRIBUTIONS

ECOLOGICAL IMPORTANCE OF CROCODILIANS


Chirona, S. (2014). The impact of Nile crocodile (Crocodylus niloticus) on the communal livelihoods: a case study of areas surrounding Ruti Dam in Gunta and Buhera districts in Zimbabwe. MSc Thesis, University of South Africa.


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Biology and Evolution of Crocodylians

**DISCIPLINES:**
- Biology and Evolution of Crocodylians
- Herpetology
- Ecology
- Systematics
- Genetics
- Conservation

**KEYWORDS:**
- Alligator
- Crocodile
- Reptile
- Nesting
- Predation
- Conservation

**ABSTRACT:**

This paper presents a comprehensive review of the biology and evolution of crocodilians, focusing on their nesting behavior. The authors discuss the role of crocodilians in the ecosystem, their reproductive strategies, and the environmental factors affecting their nesting success. The review highlights the importance of understanding nest-site selection and the impacts of human activities on nesting success.

**REFERENCES:**

- Associated with the publication of a comprehensive review on the biology and evolution of crocodilians. The review provides an overview of the key findings and future areas of research in the field. The authors aim to contribute to the conservation efforts of crocodilians, emphasizing the need for sustainable management practices.

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Ecological importance of crocodylians


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Crocodylus johnstoni during the dry season. Copesia

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1996,
Appendix S1. Extant species of crocodylians grouped by region, taxonomic family, IUCN Red List designation, and selected references that provide either claims (i.e. untested in nature or lacking evidence) or observations (i.e. anecdotally observed in nature but without experimental testing) of the ecological importance of crocodylians within four broad categories: Apex predators/Keystone species, Ecosystem engineers, Cross-ecosystem linkages & Ecological indicators.

<table>
<thead>
<tr>
<th>Family*</th>
<th>Taxa</th>
<th>IUCN Red List Category**</th>
<th>Claims (untested)</th>
<th>Demonstration (experiment or observations)</th>
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<tbody>
<tr>
<td>Americas</td>
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<td>Apex predators/Keystone species</td>
<td>Apex predators/Keystone species</td>
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<td>Ecosystem engineers</td>
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<td>Cross-ecosystem linkages</td>
<td>Cross-ecosystem linkages</td>
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<td>Ecological indicators</td>
<td>Ecological indicators</td>
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<tr>
<td>A</td>
<td>Alligator mississippiensis (American alligator)</td>
<td>LC</td>
<td>Kellogg (1929); Harper (1930); McIlhenny (1935); Shoop &amp; Ruckdeschel (1990); Gunderson (1994); Bondavalli &amp; Ulanowicz (1999); Keddy et al. (2007, 2009); Strong &amp; Frank (2010); Rosenblatt et al. (2013a); Atwood et al. (2015); Hinman (2015); Nifong &amp; Lowers (2017); Gilliland et al. (2018)</td>
<td>Harper (1930); McIlhenny (1935); Loveless (1959); Carr (1973); Jones et al. (1994); Gunderson (1994); Pintor &amp; Soluk (2006)</td>
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<tr>
<td>A</td>
<td>Caiman crocodilus (spectacled caiman)</td>
<td>LC</td>
<td>Fittkau (1970, 1973); Brazaitis et al. (1998); Balaguera-Reina &amp; González-Maya (2010)</td>
<td>Brazaitis et al. (1998)</td>
</tr>
<tr>
<td>A</td>
<td>Melanosuchus niger (black caiman)</td>
<td>LC</td>
<td>Fittkau (1970, 1973); Brazaitis et al. (1998); de Miranda (2017)</td>
<td>Brazaitis et al. (1998)</td>
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<tr>
<td>A</td>
<td><em>Paleosuchus palpebrosus</em> (Cuvier's dwarf caiman)</td>
<td>LC</td>
<td>Fittkau (1970)</td>
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<tr>
<td>A</td>
<td><em>Paleosuchus trigonatus</em> (Schneider's dwarf caiman)</td>
<td>LC</td>
<td>Fittkau (1970)</td>
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<td>C</td>
<td><em>Crocodylus acutus</em> (American crocodile)</td>
<td>VU</td>
<td>Ogden <em>et al.</em> (2005); Heithaus <em>et al.</em> (2006b); Balaguera-Reina &amp; González-Mayá (2010)</td>
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<td>C</td>
<td><em>Crocodylus intermedius</em> (Orinoco crocodile)</td>
<td>CR</td>
<td>de Miranda (2017)</td>
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<tr>
<td>C</td>
<td><em>Crocodylus moreletii</em> (Morelet's crocodile)</td>
<td>LC</td>
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</tbody>
</table>

**References:**

A: Campbell (1972); Magnusson *et al.* (1987); Brazaitis & Watanabe (2011); Campos & Mourão (2015)

B: Magnusson *et al.* (1987); Brazaitis & Watanabe (2011); Campos & Mourão (2015)

C: Campbell (1972); Medem (1981); Thorbjarnarson (1988); Kushlan & Mazzotti (1989); Mazzotti (1989); Ortiz *et al.* (1997); Mazzotti & Brandt (1994); Platt & Thorbjarnarson (2000); Casas-Andreu & Quiroz (2003); Villegas & Schnitter-Soto (2008); Wheatley (2010); Brazaitis & Watanabe (2011); Wheatley *et al.* (2012); Platt *et al.* (2013); Venegas-Anaya *et al.* (2015); Balaguera-Reina *et al.* (2016, 2018)

Wu *et al.* (2000a); Mazzotti *et al.* (2007, 2009); Rainwater *et al.* (2007); Charnau *et al.* (2010)
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<tr>
<th>Region</th>
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<th>Status</th>
<th>Authors</th>
<th>Reference</th>
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<tbody>
<tr>
<td>Africa</td>
<td><em>Crocodylus rhombifer</em> (Cuban crocodile)</td>
<td>CR</td>
<td>de Miranda (2017)</td>
<td>Campbell (1972); Thorbjarnarson (1990); Brazaitis &amp; Watanabe (2011)</td>
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<td></td>
<td><em>Crocodylus niloticus</em> (Nile crocodile)</td>
<td>LC</td>
<td>de Miranda (2017)</td>
<td>Vitt &amp; Caldwell (2014)</td>
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<td></td>
<td><em>Osteolaemus osborni</em> (Congo dwarf crocodile)</td>
<td>NA***</td>
<td>Shirley et al. (2009)</td>
<td>Campbell (1972); Waitkuwait (1985); Brazaitis &amp; Watanabe (2011)</td>
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<td></td>
<td><em>Osteolaemus tetraspis</em> (African dwarf crocodile)</td>
<td>VU</td>
<td>de Miranda (2017)</td>
<td>Campbell (1972); Brazaitis &amp; Watanabe (2011)</td>
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<td>Asia &amp; Austral-Papua</td>
<td><em>Alligator sinensis</em> (Chinese alligator)</td>
<td>CR</td>
<td>Shirley et al. (2009)</td>
<td>Campbell (1972); Brazaitis &amp; Watanabe (2011)</td>
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<tr>
<td>C</td>
<td>Crocodylus johnstoni (Australian freshwater crocodile)</td>
<td>LC</td>
<td>Vitt &amp; Caldwell (2014)</td>
<td>Campbell (1972); Webb &amp; Manolis (1980); Tucker et al. (1996, 1997b); Brazaitis &amp; Watanabe (2011); Somaweera, Webb, &amp; Shine (2011)</td>
</tr>
<tr>
<td>C</td>
<td>Crocodylus palustris (mugger crocodile)</td>
<td>VU</td>
<td>Heithaus et al. (2008b); Doody (2009); Fijn (2013); de Miranda (2017)</td>
<td>Heithaus et al. (2008b); Vitt &amp; Caldwell (2014)</td>
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<tr>
<td>C</td>
<td>Crocodylus porosus (estuarine crocodile)</td>
<td>LC</td>
<td>de Miranda (2017)</td>
<td>de Miranda (2017)</td>
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<tr>
<td>C</td>
<td>Crocodylus palustris (mugger crocodile)</td>
<td>VU</td>
<td>Heithaus et al. (2008b); Doody (2009); Fijn (2013); de Miranda (2017)</td>
<td>Heithaus et al. (2008b); Vitt &amp; Caldwell (2014)</td>
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<tr>
<td>C</td>
<td>Crocodylus porosus (estuarine crocodile)</td>
<td>LC</td>
<td>de Miranda (2017)</td>
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<td>Family</td>
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<tr>
<td>C</td>
<td><em>Crocodylus siamensis</em> (Siamese crocodile)</td>
<td>CR</td>
<td>Staniewicz et al. (2018)</td>
<td>Campbell (1972); Platt et al. (2006b, 2012); Brazaitis &amp; Watanabe (2011); Behler et al. (2018); Staniewicz et al. (2018)</td>
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</table>

* Family abbreviations: A, Alligatoridae; C, Crocodylidae; G, Gavialidae.
**IUCN Red List category abbreviations: NA, Not assessed; LC, Least Concern; VU, Vulnerable; CR, Critically Endangered.
***Assessments in progress; will appear on the 2020 Red List.
Appendix S2. Search terms used in Web of Science in July 2019 to quantify the amount of published research effort dedicated to understanding the ecological roles of different groups of large predators

We conducted a search, using the platform Web of Science, to quantify the amount of published research effort dedicated to understanding the ecological roles of different groups of large-bodied predators. Our search included all English-language scientific articles indexed by Web of Science between 1991 and June 2019. In each search we combined search terms for different large-bodied predator groups (i.e. crocodylians, canids, ursids, felids, elasmobranchs, cetaceans, and pinnipeds) with search terms related to known predator ecological roles (e.g. keystone, cascade, indicator, engineer). The full list of search terms used are:

TS=((“crocodil*” OR “alligator*” OR “gharial*” OR “caiman*” NOT (“alligator gar*” OR “alligator weed*” OR “crocodile fish*”)) AND (“keystone” OR “apex predator*” OR “top down” OR “cascade*” OR “trophic*” OR “engineer*” OR “movement*” OR “indicator*” OR “contamin*” OR “cross ecosystem*” OR “sentinel*” OR “bioindicat*” OR “ecotox*” OR “density mediate*” OR “trait mediate*”)) = 791

TS=(“canid*” OR “wolf” OR “wolves” OR “dingo*” OR “coyote*” OR “jackal*” OR “fox*”) AND (“keystone” OR “apex predator*” OR “top down” OR “cascade*” OR “trophic*” OR “engineer*” OR “movement*” OR “indicator*” OR “contamin*” OR “cross ecosystem*” OR “sentinel*” OR “bioindicat*” OR “ecotox*” OR “density mediate*” OR “trait mediate*”)) = 5,141

TS=(“ursid*” OR “bear*” NOT “bearcat*”) AND (“keystone” OR “apex predator*” OR “top down” OR “cascade*” OR “trophic*” OR “engineer*” OR “movement*” OR “indicator*” OR “contamin*” OR “cross ecosystem*” OR “sentinel*” OR “bioindicat*” OR “ecotox*” OR “density mediate*” OR “trait mediate*”)) = 24,049

TS=(“felid*” OR “lion*” OR “tiger*” OR “jaguar*” OR “leopard*” OR “serval*” OR “caracal*” OR “ocelot*” OR “bobcat*” OR “lynx” OR “cheetah*” OR “cougar*” OR “jaguarundi*” OR “panther*” OR “puma*”) AND (“keystone” OR “apex predator*” OR “top down” OR “cascade*” OR “trophic*” OR “engineer*” OR “movement*” OR “indicator*” OR “contamin*” OR “cross ecosystem*” OR “sentinel*” OR “bioindicat*” OR “ecotox*” OR “density mediate*” OR “trait mediate*”)) = 4,084

TS=(“elasmobranch*” OR “shark*”) AND (“keystone” OR “apex predator*” OR “top down” OR “cascade*” OR “trophic*” OR “engineer*” OR “movement*” OR “indicator*” OR “contamin*” OR “cross ecosystem*” OR “sentinel*” OR “bioindicat*” OR “ecotox*” OR “density mediate*” OR “trait mediate*”)) = 2,475

TS=(“cetacea*” OR “whale*” OR “dolphin*” OR “orca*” OR “porpoise*” OR “narwhal*”) AND (“keystone” OR “apex predator*” OR “top down” OR “cascade*” OR “trophic*” OR “engineer*” OR “movement*” OR “indicator*” OR “contamin*” OR “cross ecosystem*” OR “sentinel*” OR “bioindicat*” OR “ecotox*” OR “density mediate*” OR “trait mediate*”)) = 4,023

TS=((“pinniped*” OR “seal*” OR “walrus*” OR “sea lion*”) AND (“keystone” OR “apex predator*” OR “top down” OR “cascade*” OR “trophic*” OR “engineer*” OR “movement*” OR “indicator*” OR “contamin*” OR “cross ecosystem*” OR “sentinel*” OR “bioindicat*” OR “ecotox*” OR “density mediate*” OR “trait mediate*”)) = 7,945

We found that crocodylians as a group have garnered much less research focus than any of the other large predator groups included in our search (see Fig. 2). There have been 791 articles focusing in some way on
crocodylian ecological roles, but more than three times as many articles focused on elasmobranchs and more than 30 times as many articles focused on ursids. This simple analysis confirms that the ecological roles of large terrestrial and marine predator groups are well supported by relatively large bodies of research. In comparison, large freshwater predators, such as crocodylians, are still relatively poorly studied.
Appendix S3. Positive non-ecological value of crocodylians

In present-day western democratic societies, policies designed to solve environmental problems, including conservation, are unlikely to succeed unless they have broad public support and social acceptance. Priorities for conservation funding are often determined largely by the general public’s perceptions of what is ‘worth saving’ (Shine, 2011). In this context, combining economic, cultural, and intrinsic reasons may be a far more effective driver for crocodylian conservation than ecological explanations alone.

(1) Economic value

The skins of some crocodylian species are in high demand for luxury leather products and, together with meat production, their sales generate hundreds of millions of dollars annually (Caldwell, 2017; Joanen et al., 1997). Crocodylians are also tourism icons in some parts of the world, including Africa (Pringle, 2017), Australia (Tremblay, 2003), and Southeast Asia (Cohen, 2019), and are targets for the trophy hunting industry, particularly in Africa and the USA (Lindsey et al., 2007). Despite many of these harvests and uses being regulated for sustainability, in many African, Asian, and South American countries unregulated harvest as bushmeat, for both subsistence (Eaton, 2010; Efoakondza, 1993) and commercial purposes (Klemens & Thorbjarnarson, 1995; Parry et al., 2014), is common and remains a conservation problem (Thorbjarnarson, 1999). In some places, economic value derived through sustainable use programs, that provide tangible benefits to local people, is the most effective way to achieve the net positive attitudes needed to sustain crocodylian conservation efforts (McCauley, 2006). In many countries this goes hand-in-hand with management efforts to reduce the negative values crocodiles generate in communities through attacks on people and livestock, so ‘problem crocodile’ removal programs are commonplace (Fukuda et al., 2014). Where financial benefits from their conservation can also alleviate poverty and improve livelihoods, fundamental humanitarian obligations under the UN Sustainable Development Goals, the benefits are even greater (Revol, 1995). In general, the species of crocodylians that have commercial value in international trade receive significantly more conservation attention and actions than those that do not (Webb, 2014). More than 40 nations worldwide have crocodylian management programs based on some form of regulated commercial use (Thorbjarnarson, 1999). It is not surprising that the most economically valuable species are also the best studied ecologically; more funding is available for basic
research that has direct and indirect relevance to improving sustainability and commercial benefit.

(2) Cultural value
Crocodylians have aesthetic, recreational, spiritual, and psychological value in many human societies, particularly in indigenous cultures, all entwined intimately with their ecological value as perceived by local people (Moiser & Barber, 1994; Olupona, 1993; Passariello, 1999; van der Ploeg *et al.*, 2011b). Crocodylians may be symbols of sexual fertility, physical power, divinity, and productivity, all associated with different belief systems (de Silva, 2013; van der Ploeg *et al.*, 2011a). In parts of Laos, Timor Leste, and northern Australia, crocodiles are thought to embody the spirits of dead ancestors and hence are venerated in those communities (Brackhane *et al.*, 2018; Platt *et al.*, 2018). The importance of freshwater crocodiles in Australian Aboriginal culture is reflected in a complex system of totems and ceremonies that are still evident in northern Australia (Lanhupuy, 1987). Throughout West Africa crocodylians are perceived to be the sole reason for the existence of water bodies and, should they disappear, the rivers would dry up (Shirley *et al.*, 2009; Toonen, 2003). The cultural value of crocodylians is not restricted to indigenous cultures; American alligators are an important cultural symbol in the southeast USA, where many academic institutions and private businesses use the alligator as their mascot (Ribnick, 1989).

(3) Intrinsic value
Beyond any strictly ecological value, it is not uncommon for crocodylians to be perceived by humans as having intrinsic value. That is, they have a value as an entity in and of themselves, for what they are, regardless of whether or not they are instrumentally useful to humankind. For example, in a remote rural area in the Philippines, 93% of 549 people agreed with the proposition that ‘crocodiles have the right to live’ (van der Ploeg *et al.*, 2011b). This contrasts with utility or instrumental values deriving from there being a desirable end-value (Pearson, 2016). These value systems are not mutually exclusive as many people appreciate both value systems.