


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

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I. INTRODUCTION

Large-bodied predators, such as sharks, bears, wolves, big cats, and crocodylians, 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),

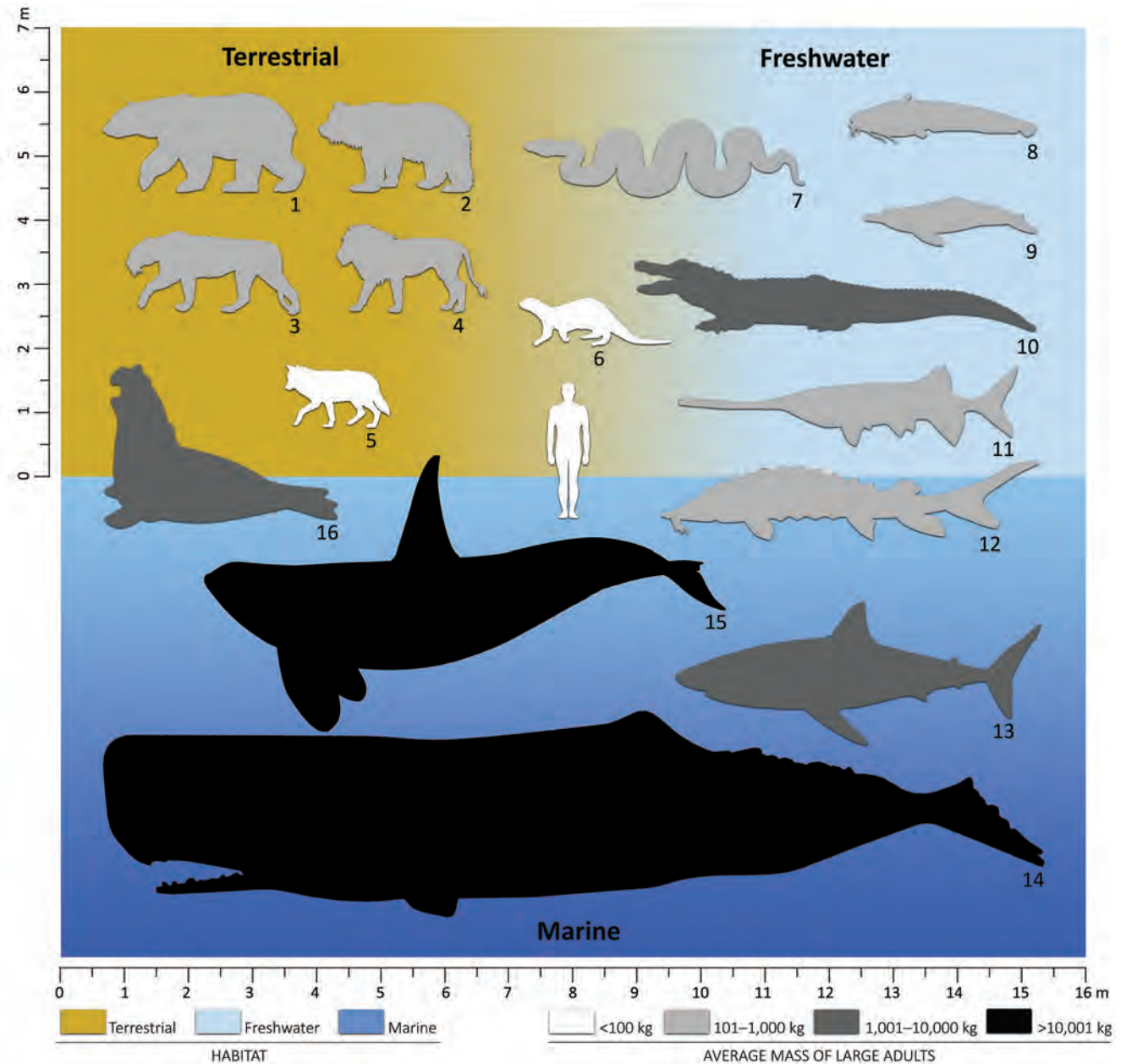


Fig. 1. Comparison of body size and mass of representative large vertebrate predators in the terrestrial, freshwater, and marine environments of the world. Silhouettes to scale based on the largest confirmed records: (1) polar bear *Ursus maritimus*; (2) kodiak bear *Ursus arctos middendorffi*; (3) Bengal 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 *Psephurus gladius*; (12) beluga sturgeon *Huso huso*; (13) great white shark *Carcharodon carcharias*; (14) sperm whale *Physeter microcephalus*; (15) orca *Orcinus orca*; (16) southern elephant seal *Mirounga leonine*.

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 crocodyliformes, 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 crocodylian conservation efforts (Mcneely & 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–crocodylian 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.

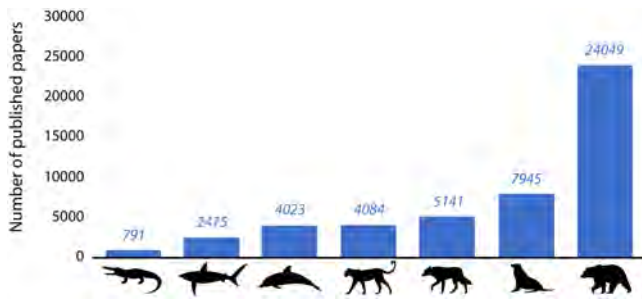


Fig. 2. A comparison of research effort on the ecological roles of different groups of large-bodied predators. Crocodylians, elasmobranchs, cetaceans, felids, canids, pinnipeds, and ursids are shown from left to right. Paper counts are based on targeted key word searches for each predator group using *Web of Science* in June 2019. The full list of search terms is given in Appendix S2.

II. CAN CROCODYLIANS 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 (v) 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 (Swanepoel, 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.*, 2015; 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.



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 status, 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.

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

[e.g. *A. mississippiensis* (Woodward *et al.*, 1984), *C. acutus* (Thorbjarnarson, 2010), Nile crocodile *C. niloticus* (Cott, 1961), gharial *Gavialis gangeticus* (Rao & Singh, 1993)]. 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 rubriventris* (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.



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 \times 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.

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

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 crocodylian will cease feeding altogether during winter, when ambient temperatures drop below the thermal 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 crocodyliforms have had varied diets (Melstrom & Irmí, 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; Waitkuwait, 1986; Ouboter, 1996; Luiselli, Akani & Capizzi, 1999; Riley & Huchzermeyer, 2000; Pauwels, Barr & Sanchez, 2007; Rice *et al.*, 2007a; Borteiro *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. $\delta^{15}\text{N}$: 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 & Wilmers, 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 & Meeuwig, 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 American 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 irrorata*) 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; Burtner, 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 hatchling 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 & Collopy, 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, Kinler & 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 crocodiles in a river actually increases the yield of fish...Crocodyles 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-valuable 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,



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).

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 & Wilmers, 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

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; Schmitz *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 & Sonneman, 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

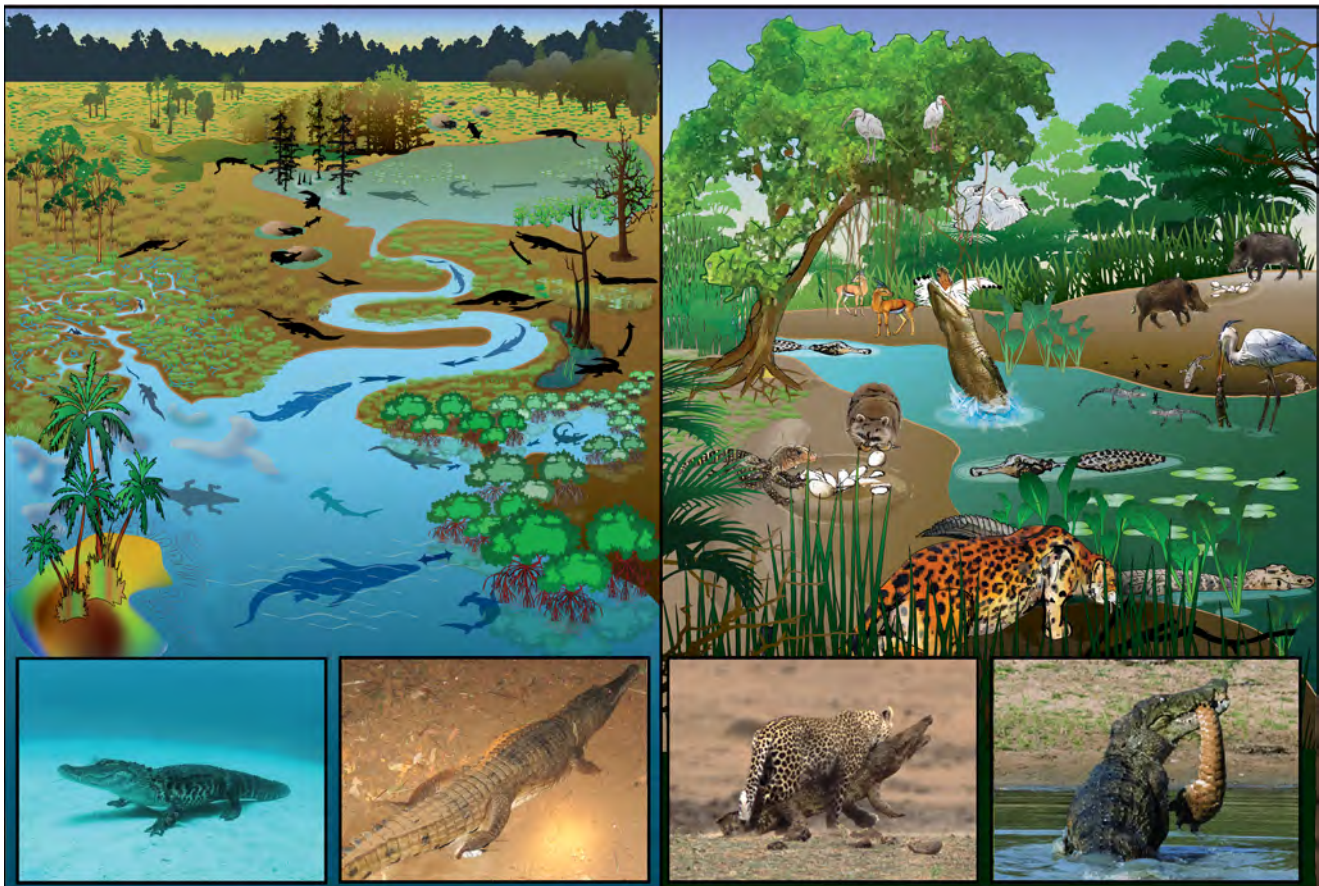


Fig. 6. Behaviours and interactions that exemplify crocodylians as mediators of cross-ecosystem fluxes and functional linkages. Left panel shows cross-ecosystem linkages established by the movement of crocodylians between and among disparate ecosystems. Several species of crocodylians repeatedly move between different aquatic habitats (fresh water, 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 (Subaluský, Fitzgerald & Smith, 2009), but this has yet to be clearly demonstrated. Recent studies on American alligators (Rosenblatt & Heithaus, 2011; Rosenblatt *et al.*, 2013a; Nifong & 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, 1985).

Based on anecdotal observations and information from local residents, Fittkau (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 (Fittkau, 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 (Subaluský *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 (Gnaspini & 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 epibionts (Monroe & Garrett, 1979; Magnusson, 1985; Cupul-Magaña *et al.*, 2011), and in reducing the spread of disease by scavenging (Subaluský *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

Tool category	How crocodylians are used	Crocodylian example
Conservation symbols (Flagship species)	Use crocodylians as icons, emblems, or symbols for conservation initiatives to harness public support for biodiversity conservation	Philippine crocodile (<i>Crocodylus mindorensis</i>) 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 <i>et al.</i> , 2011b)
Conservation of priority areas (Umbrella species)	Presence of rare and threatened crocodylians informs placement of priority conservation areas to conserve biodiversity	Gharial (<i>Gavialis gangeticus</i>) conservation efforts at National Chambal Sanctuary in India benefits numerous other species in the river system (Nair & Krishna, 2013; Sharma & Singh, 2015; Singh & Rao, 2017). Protecting West African crocodile (<i>C. suchus</i>) in isolated water bodies in Mauritania (West Africa) benefits other water-dependent species in desert environments (Velo-Antón <i>et al.</i> , 2014)
Monitoring the status of biodiversity (Indicator species)	Routine evaluation of crocodylian presence or population status used as a proxy for monitoring erosion of biodiversity, ecological integrity, or status of biodiversity	Gharial numbers used as an indicator of the health of the Ganga river ecosystem in India (Behera, Singh & Sagar, 2014), and American alligators (<i>Alligator mississippiensis</i>) in the Everglades restoration project (Cherkiss <i>et al.</i> , 2006)
Generation of revenues and income	Presence of crocodylians for consumptive and non-consumptive commercial use provides incentive to maintain natural state of ecosystems and preserve other elements of biodiversity	Harvesting common caiman (<i>Caiman crocodylus</i>) in large ranches in Venezuela is a basis for effective wildlife conservation and sustainable wildlife use (Hoogesteijn & Chapman, 1997)

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 crocodylian ecology and conservation community to implement question- or hypothesis-driven research linking crocodylian 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 crocodylian 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 involved in such decisions, benefiting the future of crocodylians in particular, and the conservation and resilience of freshwater ecosystems across the planet more generally.

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

R.S., G.G., and B.L.W. devised the conceptual idea and outline; R.S., J.N., A.R., J.v.d.P., G.G., and B.L.W. made substantial contributions to drafting the manuscript, acquiring literature, and interpreting results; J.N. and A.R. compiled Table 1; R.S. and J.N. prepared the figures; M.T., A.P., M.L.B., W.E.M., R.M.E., S.G.P., M.H.S., F.J.M. and R.W. developed specific sections with revisions, literature,

and comments; all authors participated in drafting the final version of the manuscript; G.G., G.W., J.N., A.R., M.H.S. and B.L.W. critically revised the manuscript; and all authors gave final approval of the submitted and revised versions.

XII. REFERENCES

References identified with asterisks are used in the supporting information.

- ADAME, M. F., JARDINE, T. D., FRY, B., VALDEZ, D., LINDNER, G., NADJI, J. & BUNN, S. E. (2018). Estuarine crocodiles in a tropical coastal floodplain obtain nutrition from terrestrial prey. *PLoS One* **13**, e0197159.
- *ADUGNA, C., KIROS, S., DEJENE, T., ASMELASH, T. & HADGU, K. M. (2017). Distribution and habitat suitability of Nile crocodile (*Crocodilus niloticus*, L. 1768) in Tekeze River Dam, Tigray, Ethiopia. *International Journal of Biodiversity and Conservation* **9**, 350–362.
- ALLAN, J. D., ABELL, R., HOGAN, Z., REVENGA, C., TAYLOR, B. W., WELCOMME, R. L. & WINEMILLER, K. (2005). Overfishing of inland waters. *Bioscience* **55**, 1041–1051.
- *ALLSTEADT, J. (1994). Nesting Ecology of *Caiman crocodilus* in Caño Negro, Costa Rica. *Journal of Herpetology* **28**, 12–19.
- ANDERSON, W. B. & POLIS, G. A. (1999). Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* **118**, 324–332.
- ARRIGUÍN-SÁNCHEZ, F. (2011). Ecosystem dynamics under "top-down" and "bottom-up" control situations generated by intensive harvesting rates. *Hidrobiológica* **21**, 323–332.
- ASHTON, P. J. (2010). The demise of the Nile crocodile (*Crocodilus 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.
- *ATWOOD, T. B., HAMMILL, E., KRATINA, P., GREIG, H. S., SHURIN, J. B. & RICHARDSON, J. S. (2015). Warming alters food web-driven changes in the CO₂ flux of experimental pond ecosystems. *Biology Letters* **11**, 20150785.
- AUDUBON, J. J. (1827). Observations on the natural history of the alligator. *Edinburgh New Philosophical Journal* **2**, 270–280.
- *DE AZEVEDO, F. C. C. & MURRAY, D. L. (2007). Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. *Biological Conservation* **137**, 391–402. Elsevier.
- *BALAGUERA-REINA, S. A. & GONZÁLEZ-MAYA, J. F. (2010). Percepciones, conocimiento y relaciones entre los Crocodylia y poblaciones humanas en la Vía Parque Isla de Salamanca y su zona de amortiguamiento, Caribe colombiano. *Revista Latinoamericana de Conservación* **1**, 53–63.
- *BALAGUERA-REINA, S. A., VENEGAS-ANAYA, M., SÁNCHEZ, A., ARBELAEZ, I., LESSIOS, H. A. & DENSMORE, L. D. (2016). Spatial ecology of the American crocodile in a tropical Pacific Island in Central America. *PLoS One* **11**, 1–20.
- BALAGUERA-REINA, S. A., VENEGAS-ANAYA, M., BELTRÁN-LÓPEZ, V., CRISTANCHO, A. & DENSMORE, L. D. (2018). Food habits and ontogenetic dietary partitioning of American crocodiles in a tropical Pacific Island in Central America. *Ecosphere* **9**, e02393.
- *BANGMA, J. T., BOWDEN, J. A., BRUNELL, A. M., CHRISTIE, I., FINNELL, B., GUILLETTE, M. P., JONES, M., LOWERS, R. H., RAINWATER, T. R., REINER, J. L., WILKINSON, P. M. & GUILLETTE, L. J. (2017). Perfluorinated alkyl acids in plasma of American alligators (*Alligator mississippiensis*) from Florida and South Carolina. *Environmental Toxicology and Chemistry* **36**, 917–925.
- *BANKS, C. (2005). *National Recovery Plan for the Philippine Crocodile, Crocodylus Mindorensis 2005–2008*. Quezon City, Philippines.
- *BARO-NÓBREGA, J. A. L., MARIONI, B., VILLAMARÍN, F., SOARES, A. M. V. M., MAGNUSSON, W. E. & DA SILVEIRA, R. (2014). Researcher disturbance has minimal impact on natural predation of caiman nests in central Amazonia. *Journal of Herpetology* **48**, 338–342.
- BARLEY, S. C., MEEKAN, M. G. & MEEUWIG, J. J. (2017). Species diversity, abundance, biomass, size and trophic structure of fish on coral reefs in relation to shark abundance. *Marine Ecology Progress Series* **565**, 163–179.
- BARTELS, P., CUCHEROUSET, J., STEGER, K., EKLÓV, P., TRANVIK, L. J. & HILLEBRAND, H. (2012). Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* **93**, 1173–1182.
- BARTRAM, W. (1980). *Travels through North & South Carolina, Georgia, East & West Florida, the Cherokee Country*. James & Johnson, Philadelphia, PA.
- BEHERA, S. K., SINGH, H. & SAGAR, V. (2014). Indicator species (gharial and dolphin) of riverine ecosystem: an exploratory of river Ganga. In *Our National River Ganga* (ed R. Sanghi), pp. 121–141. Springer, Cham, Switzerland.
- *BEHLER, N., KOPSIEKER, L., STANIEWICZ, A., DARMANSYAH, S., STUEBING, R. & ZIEGLER, T. (2018). Population size, demography and feeding preferences of the Siamese crocodile *Crocodilus siamensis* (Schneider, 1801) in the Mesangat Swamp in Kalimantan, Indonesia. *Raffles Bulletin of Zoology* **66**, 506–516.
- BESCHTA, R. L. & RIPPLE, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* **142**, 2401–2414.
- *BHATNAGAR, C. & MAHUR, M. (2010). Observations on feeding behavior of a wild population of Marsh Crocodile in Baghdarrah Lake, Udaipur, Rajasthan. *Reptile Rap* **10**, 27–28.
- *BISHOP, J. M., LESLIE, A. J., BOURQUIN, S. L. & O'RYAN, C. (2009). Reduced effective population size in an overexploited population of the Nile crocodile (*Crocodilus niloticus*). *Biological Conservation* **142**, 2335–2341.
- *BOGGS, A. S. P., HAMLIN, H. J., NIFONG, J. C., KASSIM, B. L., LOWERS, R. H., GALLIGAN, T. M., LONG, S. E. & GUILLETTE, L. J. (2016). Urinary iodine and stable isotope analysis to examine habitat influences on thyroid hormones among coastal dwelling American alligators. *General and Comparative Endocrinology* **226**, 5–13.
- BONDAVALLI, C. & ULANOWICZ, R. E. (1999). Unexpected effects of predators upon their prey: the case of the American alligator. *Ecosystems* **2**, 49–63.
- BORTEIRO, C., GUTIÉRREZ, F., TEDROS, M. & KOLENC, F. (2009). Food habits of the broad-snouted Caiman (*Caiman latirostris*: Crocodylia, Alligatoridae) in northwestern Uruguay. *Studies on Neotropical Fauna and Environment* **44**, 31–36.
- *BOURQUIN, S. L. (2007). *The population ecology of the Nile crocodile (Crocodylus niloticus) in the panhandle region of the Okavango Delta, Botswana*. Doctoral Dissertation: University of Stellenbosch, Stellenbosch, South Africa.
- BRACKHANE, S., WEBB, G., XAVIER, F. M., GUSMAO, M. & PECHACEK, P. (2018). When conservation becomes dangerous: human-crocodile conflict in Timor-Leste. *The Journal of Wildlife Management* **82**, 1332–1344.
- BRACKHANE, S., WEBB, G., XAVIER, F. M., TRINDADE, J., GUSMAO, M. & PECHACEK, P. (2019). Crocodile management in Timor-Leste: drawing upon traditional ecological knowledge and cultural beliefs. *Human Dimensions of Wildlife* **24**, 314–331.
- BRACZKOWSKI, A. R., O'BRYAN, C. J., STRINGER, M. J., WATSON, J. E., POSSINGHAM, H. P. & BEYER, H. L. (2018). Leopards provide public health benefits in Mumbai, India. *Frontiers in Ecology and the Environment* **16**, 176–182.
- BRANDT, L. A., BEAUCHAMP, J., BROWDER, J. A., CHERKISS, M., CLARKE, A., DOREN, R. F., FREDERICK, P., GAISER, E., GAWLIK, D., GLENN, L., HARDY, E., HAYNES, A. L., A. HUEBNER, HART, K., KELBLE, C. et al. (2014). *System-wide indicators for Everglades restoration. 2014 Report*, pp. 111. Unpublished Technical Report.
- BRANDT, L. A., BEAUCHAMP, J. S., JEFFERY, B. M., CHERKISS, M. S. & MAZZOTTI, F. J. (2016). Fluctuating water depths affect American alligator (*Alligator mississippiensis*) body condition in the Everglades, Florida, USA. *Ecological Indicators* **67**, 441–450.
- *BRAZAITIS, P. & WATANABE, M. E. (2011). Crocodylian behaviour: a window to dinosaur behaviour? *Historical Biology* **23**, 73–90.
- *BRAZAITIS, P., REBELO, G. H., YAMASHITA, C., ODIERNA, E. A. & WATANABE, M. E. (1996). Threats to Brazilian crocodylian populations. *Oryx* **30**, 275–284.
- *BRAZAITIS, P., WATANABE, M. E. & AMATO, G. (1998). The caiman trade. *Scientific American* **278**, 70–76.
- *BRIEN, M. L., READ, M. A., MCCALLUM, H. I. & GRIGG, G. C. (2008). Home range and movements of radio-tracked estuarine crocodiles (*Crocodilus porosus*) within a non-tidal waterhole. *Wildlife Research* **35**, 140–149.
- BRITO, J. C., MARTÍNEZ-FREIRÍA, F., SIERRA, P., SILLERO, N. & TARROSO, P. (2011). Crocodiles in the Sahara Desert: an update of distribution, habitats and population status for conservation planning in Mauritania. *PLoS One* **6**, e14734.
- BRODEUR, V., OUELLET, J.-P., COURTOIS, R. & FORTIN, D. (2008). Habitat selection by black bears in an intensively logged boreal forest. *Canadian Journal of Zoology* **86**, 1307–1316.
- *BUAH-KWOFIE, A., HUMPHRIES, M. S., COMBRINK, X. & MYBURGH, J. G. (2018). Accumulation of organochlorine pesticides in fat tissue of wild Nile crocodiles (*Crocodilus niloticus*) from iSimangaliso Wetland Park, South Africa. *Chemosphere* **195**, 463–471.
- *BUCOL, A. A., MANALO, R. I., MERCADO, V. P., BELO, W. T., CHAN, S. S., BANTAYAN, D. C. & ORIENTAL, N. (2014). Do crocodiles benefit local fishery productivity in The Philippines? In *Proceedings of the 23rd Working Meeting of the IUCN/SSC Crocodile Specialist Group*, pp. 306–316. IUCN, Gland, Switzerland.
- *BUENFIL-ROJAS, A. M., LVAREZ-LEGORRETA, T. & CEDEÑO-VÁZQUEZ, J. R. (2015). Metals and metallothioneins in Morelet's crocodile (*Crocodilus moreletii*) from a transboundary river between Mexico and Belize. *Archives of Environmental Contamination and Toxicology* **68**, 265–273.
- *BUENFIL-ROJAS, A. M., ALVAREZ-LEGORRETA, T. & CEDEÑO-VÁZQUEZ, J. R. (2018). Mercury and metallothioneins in blood fractions and tissues of captive Morelet's crocodiles in Quintana Roo, Mexico. *Chemosphere* **199**, 630–636.
- BUFFETAUT, E. (1979). The evolution of the crocodylians. *Scientific American* **241**, 130–145.
- BURKHARD, B., MÜLLER, F. & LILL, A. (2008). Ecosystem health indicators. In *Ecological Indicators* (eds S. E. JORGENSEN and B. D. FATH), pp. 1132–1138. Elsevier, Oxford, UK.
- BURTNER, B. F. (2011). Symbiosis between long legged wading birds (Ciconiiformes) and alligators (*Alligator mississippiensis*): Testing the 'nest protector' hypothesis. MSC Thesis. University of Florida, Florida.

- BUSCH, D. E. & TREXLER, J. C. (2002). *Monitoring Ecosystems: Interdisciplinary Approaches for Evaluating Ecoregional Initiatives*. Island Press, Washington, D.C.
- *CALDWELL, J. (2017). *World Trade in Crocodylian Skins 2013–2015*. UNEP-WCMC, Cambridge.
- *CALVERLEY, P. M. & DOWNS, C. T. (2015). Movement and home range of Nile crocodiles in Ndumo game reserve, South Africa. *Koedoe* **57**, 1–13.
- *CALVERLEY, P. M. & DOWNS, C. T. (2017). The past and present nesting ecology of Nile crocodiles in Ndumo Game Reserve, South Africa: reason for Concern? *Journal of Herpetology* **51**, 19–26.
- CAMPBELL, H. W. (1972). Ecological or phylogenetic interpretations of crocodylian nesting habits. *Nature* **238**, 404.
- CAMPBELL, K. R. (2003). Ecotoxicology of crocodylians. *Applied Herpetology* **1**, 45–163.
- CAMPBELL, M. R. & MAZZOTTI, F. J. (2004). Characterization of natural and artificial alligator holes. *Southeastern Naturalist* **3**, 583–594.
- *CAMPBELL, H. A., MICHELI, M. A. & ABE, A. (2008). A seasonally dependent change in the distribution and physiological condition of *Caiman crocodylus yacare* in the Paraguyan River Basin. *Wildlife Research* **35**, 150–157.
- CAMPBELL, H. A., WATTS, M. E., SULLIVAN, S., READ, M. A., CHOUKROUN, S., IRWIN, S. R. & FRANKLIN, C. E. (2010a). Estuarine crocodiles ride surface currents to facilitate long-distance travel. *Journal of Animal Ecology* **79**, 955–964.
- *CAMPBELL, J. W., WATERS, M. N., TARTER, A. & JACKSON, J. (2010b). Heavy metal and selenium concentrations in liver tissue from wild American alligator (*Alligator mississippiensis*) livers near Charleston, South Carolina. *Journal of Wildlife Diseases* **46**, 1234–1241.
- CAMPBELL, H. A., DWYER, R. G., IRWIN, T. R. & FRANKLIN, C. E. (2013). Home range utilisation and long-range movement of estuarine crocodiles during the breeding and nesting season. *PLoS One* **8**, e62127.
- CAMPOS, Z. (1993). Effect of habitat on survival of eggs and sex ratio of hatchlings of *Caiman crocodylus yacare* in the Pantanal, Brazil. *Journal of Herpetology* **27**, 127–132.
- *CAMPOS, Z. & MAGNUSON, W. (1995). Relationships between rainfall nesting habitat and fecundity of *Caiman crocodylus yacare* in the Pantanal. *Journal of Tropical Ecology* **11**, 351–358.
- CAMPOS, Z. & MAGNUSON, W. E. (2013). Thermal relations of dwarf caiman, *Paleosuchus palpebrosus*, in a hillside stream: evidence for an unusual thermal niche among crocodylians. *Journal of Thermal Biology* **38**, 20–23.
- *CAMPOS, Z. & MOURO, G. (2015). Camera traps capture images of predators of *Caiman crocodylus yacare* eggs (Reptilia: Crocodylia) in Brazil's Pantanal wetlands. *Journal of Natural History* **49**, 977–982.
- *CAMPOS, Z., COUTINHO, M. & MAGNUSON, W. E. (2003). Terrestrial activity of caiman in the Pantanal, Brazil. *Copeia* **2003**, 628–634.
- *CAMPOS, Z., COUTINHO, M., MOURO, G., BAYLISS, P. & MAGNUSON, W. E. (2006). Long distance movements by *Caiman crocodylus yacare*: implications for management of the species in the Brazilian Pantanal. *Herpetological Journal* **16**, 123–132.
- *CAMPOS, Z., SANAIOTTI, T., MARQUES, V. & MAGNUSON, W. E. (2015). Geographic variation in clutch size and reproductive season of the dwarf caiman, *Paleosuchus palpebrosus*, in Brazil. *Journal of Herpetology* **49**, 95–98.
- *CAMPOS, Z., MUNIZ, F., DESBIEZ, A. L. J. & MAGNUSON, W. E. (2016). Predation on eggs of Schneider's dwarf caiman, *Paleosuchus trigonatus* (Schneider, 1807), by armadillos and other predators. *Journal of Natural History* **2933**, 1–6.
- CANNING, A. & DEATH, R. (2017). Trophic cascade direction and flow determine network flow stability. *Ecological Modelling* **355**, 18–23.
- CARIGNAN, V. & VILLARD, M.-A. (2002). Selecting indicator species to monitor ecological integrity: a review. *Environmental Monitoring and Assessment* **78**, 45–61.
- CARPENTER, S. R. & KITCHELL, J. F. (1988). Consumer control of lake productivity. *Bioscience* **38**, 764–769.
- *CARR, A. F. (1973). *The Everglades*. Time-Life Books, New York, NY.
- *CASAS-ANDREU, G. & QUIROZ, G. B. (2003). Hábitos alimenticios de *Crocodylus acutus* (Reptilia: Crocodylidae) determinados por el análisis de sus excretas en la costa de Jalisco, Mexico. *Anales del Instituto de Biología, UNAM* **74**, 35–42.
- CAUT, S., FRANCOIS, V., BACQUES, M., GUIRAL, D., LEMAIRE, J., LEPOINTE, G., MARQUIS, O. & STURARO, N. (2019). The dark side of the black caiman: shedding light on species dietary ecology and movement in Agami pond, French Guiana. *PLoS One* **14**, e0217239.
- *CHANG, M. S., GACHAL, G. S., QADRI, A. H. & SHAIKH, M. Y. (2012). Bio-ecological status, management, and conservation of marsh crocodiles (*Crocodylus palustris*) in Deh Akro 2, Sindh-Pakistan. *Sindh University Research Journal (Science Series)* **44**, 209–214.
- *CHANG, M. S., GACHAL, G. S., QADRI, A. H., KAHTOON, Z., JAFRI, S. I. H., KALHORO, M. A., MEMON, K. H. & SHEIKH, M. Y. (2014). Physico-chemical assessment and ecological impacts on marsh crocodiles in protected areas of nara thar desert khairpur. *Biharean Biologist* **8**, 24–31.
- *CHARRAU, P., THORBARNARSON, J. B. & HÉNAUT, Y. (2010). Tropical cyclones and reproductive ecology of *Crocodylus acutus* Cuvier, 1807 (Reptilia: Crocodylia: Crocodylidae) on a Caribbean atoll in Mexico. *Journal of Natural History* **44**, 741–761.
- *CHENG-KUAN, C. (1957). Observations on the life history of Chinese alligator (*Alligator sinensis* Fauvel). *Acta Zoologica Sinica* **9**, 129–143.
- CHEKISS, M. S., BRANDT, L. A., CHARTIER, K. L., LORENZ, J., MILLER, M., PARRY, M. W., PEARLSTINE, L. G., RICE, K. G., SHANG, Z. & MAZZOTTI, F. J. (2006). The role of the american crocodile (*Crocodylus acutus*) as an indicator of ecological change in everglades ecosystems. In *Greater Everglades Ecosystem Restoration Conference*, Orlando, FL.
- *CHIHONA, S. (2014). The impact of Nile crocodile (*Crocodylus niloticus*) on the communal livelihoods: a case study of areas surrounding Ruti Dam in Gutu and Buhera districts in Zimbabwe. MSc Thesis, University of South Africa.
- *CINTRA, R. (1988). Nesting ecology of the Paraguayan Caiman (*Caiman yacare*) in the Brazilian Pantanal. *Journal of Herpetology* **22**, 219–222.
- COGGAN, N. V., HAYWARD, M. W. & GIBB, H. (2018). A global database and 'state of the field' review of research into ecosystem engineering by land animals. *Journal of Animal Ecology* **87**, 974–994.
- *COHEN, E. (2019). Crocodile tourism: the emancipation of ferocity. *Tourism Culture & Communication* **19**, 83–102.
- *COMBRINK, X., WARNER, J. K. & DOWNS, C. T. (2017). Nest-site selection, nesting behaviour and spatial ecology of female Nile crocodiles (*Crocodylus niloticus*) in South Africa. *Behavioural Processes* **135**, 101–112. Elsevier B.V.
- *CORLETT, R. T. (2011). Vertebrate carnivores and predation in the Oriental (Indomalayan) Region. *The Raffles Bulletin of Zoology* **59**, 325–360.
- *CORREIA, J., CESAR, R., MARSICO, E., DINIZ, G. T. N., ZORRO, M. C. & CASTILHOS, Z. (2014). Mercury contamination in alligators (*Melanosuchus niger*) from Mamirauá Reservoir (Brazilian Amazon) and human health risk assessment. *Environmental Science and Pollution Research* **21**, 13522–13527.
- CORTÉS, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science* **56**, 707–717.
- COTT, H. B. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *The Transactions of the Zoological Society of London* **29**, 211–356.
- COTTEE-JONES, H. E. W. & WHITTAKER, R. J. (2012). Perspective: the keystone species concept: a critical appraisal. *Frontiers of Biogeography* **4**, 117–127.
- *CRAIGHEAD, F. C. (1968). The role of the alligator in shaping plant communities and maintaining wildlife in the southern Everglades. *Florida Naturalist* **41**, 67–74.
- CRAIGHEAD, F. C. (1969). The role of the alligator in shaping plant communities and maintaining wildlife in the southern Everglades. Florida Audubon Society.
- CRAWFORD, R. J., UNDERHILL, L. G., RAUBENHEIMER, C., DYER, B. & MARTIN, J. (1992). Top predators in the Benguela ecosystem—implications of their trophic position. *South African Journal of Marine Science* **12**, 675–687.
- CRESPO, R. G., BEAUCHAMP, J. S., MAZZOTTI, F. J. & CHERKISS, M. S. (2015). *Crocodylus acutus* (American crocodile) long distance juvenile movement. *Herpetological Review* **46**, 623–624.
- CRISPS (2017). Collaborative Research Initiative on Sustainability and Protection of Springs: Final Report 2014–2017. University of Florida Water Institute, USA, Submitted to St. Johns River Water Management District Springs Protection Initiative [SPI].
- CROOKS, K. R. & SOULÉ, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**, 563.
- CUPUL-MAGAÑA, F. G., RUBIO-DELGADO, A., ESCOBEDO-GALVÁN, A. H. & REYES-NUÑEZ, C. (2011). First report of the marine barnacles *Lepas anatifera* and *Chelombia testudinaria* as epibionts on American crocodile (*Crocodylus acutus*). *Herpetological Notes* **4**, 213–214.
- *DA SILVEIRA, R. & MAGNUSON, W. E. (1999). Diets of spectacled and black caiman in the Anavilhanas archipelago, Central Amazonia, Brazil. *Journal of Herpetology* **33**, 181–192.
- *DA SILVEIRA, R., RAMALHO, E. E., THORBARNARSON, J. B. & MAGNUSON, W. E. (2010). Depredation by jaguars on caimans and importance of reptiles in the diet of jaguar. *Journal of Herpetology* **44**, 418–424.
- *DABROWSKI, J., OBERHOLSTER, P. J., DABROWSKI, J. M., LE BRASSEUR, J. & GIESKES, J. (2013). Chemical characteristics and limnology of Loskop Dam on the Olifants River (South Africa), in light of recent fish and crocodile mortalities. *Water SA* **39**, 675–686.
- DAVENPORT, J., GROVE, D., CANNON, J., ELLIS, T. & STABLES, R. (1990). Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus*. *Journal of Zoology* **220**, 569–592.
- DAVIDSON, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research* **65**, 934–941.
- *DAVIS, S. M., CHILDERS, D. L., LORENZ, J. J., WANLESS, H. R. & HOPKINS, T. E. (2005). A conceptual model of ecological interactions in the mangrove estuaries of the Florida Everglades. *Wetlands* **25**, 832–842.
- DEITZ, D. C. & HINES, T. C. (1980). Alligator nesting in north-central Florida. *Copeia* **1980**, 249–258.
- DEITZ, D. C. & JACKSON, D. R. (1979). Use of American alligator nests by nesting turtles. *Journal of Herpetology* **13**, 510–512.
- *DELANY, M. F. & ABERCROMBIE, C. L. (1986). American alligator food habits in Northcentral Florida. *The Journal of Wildlife Management* **50**, 348.
- DIEFFENBACH, C. O. D. C. (1979). Ampullarid gastropod-staple food of *Caiman latirostris*? *Copeia* **1979**, 162–163.

- *DING, Y., WANG, X., HE, L., SHAO, M., XIE, W., JOHN, B. T. & SCOTT, T. M. (2001). Study on the current population and habitat of the wild Chinese alligator (*Alligator sinensis*). *Chinese Biodiversity* **9**, 102–108.
- *DOODY, J. S. (2009). Eyes bigger than stomach: prey caching and retrieval in the saltwater crocodile, *Crocodylus porosus*. *Herpetological Review* **40**, 26.
- DOREN, R. (2006). Indicators for restoration: south Florida ecosystem restoration, pp. 198. Report to the South Florida Ecosystem Restoration Task Force.
- DOREN, R. F., TREXLER, J. C., GOTTLIEB, A. D. & HARWELL, M. C. (2009). Ecological indicators for system-wide assessment of the greater everglades ecosystem restoration program. *Ecological Indicators* **9**, S2–S16.
- DUDGEON, D., ARTHINGTON, A. H., GESSNER, M. O., KAWABATA, Z.-I., KNOWLER, D. J., LÉVÊQUE, C., NAIMAN, R. J., PRIEUR-RICHARD, A.-H., SOTO, D. & STIASSNY, M. L. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**, 163–182.
- DUFFY, J. E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters* **6**, 680–687.
- DUGAN, B. A., RAND, A. S., BURGHARDT, G. M. & BOCK, B. C. (1981). Interactions between nesting crocodiles and iguanas. *Journal of Herpetology* **15**, 409–414.
- *EATON, M. (2010). Dwarf crocodile *Osteoleaemus tetraspis*. Crocodiles. Status survey and conservation action plan, 127–132.
- EDELMAN, A., GELDING, A., KONOVALOV, E., MCCOMSKIE, R., PENNY, A., ROBERTS, N., TEMPLEMAN, S., TREWIN, D., ZIEMICKI, M. & TREWIN, B. (2014). *State of the tropics: 2014 report*. James Cook University, Cairns.
- *EGGINS, S., SCHNEIDER, L., KRUKOWA, F., VOGT, R. C., DA SILVEIRA, R. & MAHER, W. (2015). Mercury concentrations in different tissues of turtle and caiman species from the Rio Purus, Amazonas, Brazil. *Environmental Toxicology and Chemistry* **34**, 2771–2781.
- ELSEY, R. M., SELMAN, W., KING, R., MILLER, M. & PLATT, S. G. (2013). *Alligator mississippiensis* (American alligator) nests used by other reptiles in Coastal Louisiana. *Herpetological Review* **44**, 659–660.
- *ELSEY, R. M., KING, R., NIFONG, J. C. & FRICK, M. G. (2014). *Alligator mississippiensis* (American alligator). Epibiosis. *Herpetological Review* **45**, 118–120.
- ELSEY, R. M., MILLER, M., LEJEUNE, D. & SELMAN, W. (2016). Commensal nesting of *Scincella lateralis* (Little brown skinks) in *Alligator mississippiensis* (American alligator) nests and *Ondatra zibethicus* (Muskrat) houses in Southwestern Louisiana. *Southeastern Naturalist* **15**, 653–668.
- ESCOBEDO-GALVÁN, A. H., CASAS-ANDREU, G., BARRIOS-QUIROZ, G., SUSTAIFA-RODRÍGUEZ, V. H. & LÓPEZ-LUNA, M. A. (2011). Observaciones sobre nidos de *Crocodylus moreletii* en San Luis Potosí, México. *Revista Mexicana De Biodiversidad* **82**, 315–317.
- *ESCOBEDO-GALVÁN, A., RETANA, J. A., MÉNDEZ, C. & GONZÁLEZ-MAYA, J. (2012). Efecto potencial del cambio climático en la proporción de sexos del caimán en Costa Rica. *Tropical Journal of Environmental Science* **44**, 49–60.
- ESPIÑOZA, M., CAPO, M., HEUPEL, M. R., TOBIN, A. J. & SIMPFENDORFER, C. A. (2014). Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. *PLoS One* **9**, e106885.
- ESTES, J. A., TERBORGH, J., BRASHARES, J. S., POWER, M. E., BERGER, J., BOND, W. J., CARPENTER, S. R., ESSINGTON, T. E., HOLT, R. D. & JACKSON, J. B. (2011). Trophic downgrading of planet earth. *Science* **333**, 301–306.
- FARLOW, J. O. & HOLTZ, T. R. (2002). The fossil record of predation in dinosaurs. *The Paleontological Society Papers* **8**, 251–266.
- FERREIRA, S. M. & PIENAAR, D. (2011). Degradation of the crocodile population in the Olifants River gorge of Kruger National Park, South Africa. *Aquatic Conservation: Marine and Freshwater Ecosystems* **21**, 155–164.
- FERRETTI, F., WORM, B., BRITTON, G. L., HEITHAUS, M. R. & LOTZE, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* **13**, 1055–1071.
- *FIJN, N. (2013). Living with crocodiles: engagement with a powerful reptilian being. *Animal Studies Journal* **2**, 1–27.
- FITTKAU, E. J. (1970). Role of caimans in the nutrient regime of mouth-lakes of Amazon affluents (an hypothesis). *Biotropica* **2**, 138.
- FITTKAU, E. J. (1973). Crocodiles and the nutrient metabolism of Amazonian waters. *Amazoniana* **4**, 103–133.
- *FLEMING, D.M., PALMISANO, A.W. & JOANEN, T. (1976). Food habits of coastal marsh raccoons with observations of alligator nest predation. In Proceedings of the Annual Conference S.E. Association of Fish & Wild Agencies pp. 348–357.
- FORTIN, D., BEYER, H. L., BOYCE, M. S., SMITH, D. W., DUCHESNE, T. & MAO, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**, 1320–1330.
- FREDERICK, P. C. & COLLOPY, M. W. (1989). The role of predation in determining reproductive success of colonially nesting wading birds in the Florida Everglades. *Condor* **91**, 860–867.
- FREDERICK, P. C. & SPALDING, M. G. (1994). Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. Everglades: the ecosystem and its restoration, 659–691.
- *FUJISAKI, I., RICE, K. G., PEARLSTINE, L. G. & MAZZOTTI, F. J. (2009). Relationship between body condition of American alligators and water depth in the Everglades, Florida. *Hydrobiologia* **635**, 329–338.
- *FUJISAKI, I., MAZZOTTI, F. J., HART, K. M., RICE, K. G., OGUURCAK, D., ROCHFORD, M., JEFFERY, B. M., BRANDT, L. A. & CHERKISS, M. S. (2012). Use of alligator hole abundance and occupancy rate as indicators for restoration of a human-altered wetland. *Ecological Indicators* **23**, 627–633.
- *FUJISAKI, I., HART, K. M., MAZZOTTI, F. J., CHERKISS, M. S., SARTAIN, A. R., JEFFERY, M. B., BEAUCHAMP, J. S. & DENTON, M. (2014). Home range and movements of American alligators (*Alligator mississippiensis*) in an estuary habitat. *Animal Biotelemetry* **2**, 1–10.
- *FUKUDA, Y. & CUFF, N. (2013). Vegetation communities as nesting habitat for the saltwater crocodiles in the Northern Territory of Australia. *Herpetological Conservation and Biology* **8**, 641–651.
- 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.
- FUKUDA, Y., MANOLIS, C. & APPEL, K. (2014). Management of human-crocodile conflict in the Northern Territory, Australia: review of crocodile attacks and removal of problem crocodiles. *The Journal of Wildlife Management* **78**, 1239–1249.
- FULTON, E. A., SMITH, A. D. & PUNT, A. E. (2005). Which ecological indicators can robustly detect effects of fishing? *ICES Journal of Marine Science* **62**, 540–551.
- GABREY, S. W., KINLER, N. & ELSEY, R. M. (2009). Impacts of nutria removal on food habits of American alligators in Louisiana. *Southeastern Naturalist* **8**, 347–354.
- GALVÁN, J. A. E., RETANA, J. A., MÉNDEZ, C. & MAYA, J. G. (2012). Efecto potencial del cambio climático en la proporción de sexos del caimán en Costa Rica. *Revista de Ciencias Ambientales* **44**, 49–60.
- *GAMES, I. (1990). *The feeding ecology of two Nile crocodile populations in the Zambezi Valley*. PhD Thesis, University of Zimbabwe, Harare, Zimbabwe.
- *GHALIB, S., RAHMAN, H., IFFAT, F. & HASNAIN, S. (1981). A checklist of the reptiles of Pakistan. *Records of the Zoological Survey of Pakistan* **8**, 37–59.
- GIBBON, J. W., SCOTT, D. E., RYAN, T. J., BUHLMANN, K. A., TUBERVILLE, T. D., METTS, B. S., GREENE, J. L., MILLS, T., LEIDEN, Y. & POPPY, S. (2000). The global decline of reptiles, Déjà Vu amphibians. *Bioscience* **50**, 653–666.
- *GILLILAND, C. R., COLVIN, M. E., RUSH, S. A. & REAGAN, S. (2018). American alligators are predators of paddlefish: an undocumented predator-prey linkage affecting paddlefish population dynamics. *Food Webs* **16**, e00087.
- GLEN, A. S., DICKMAN, C. R., SOULE, M. E. & MACKAY, B. (2007). Evaluating the role of the dingo as a trophic regulator in Australian ecosystems. *Austral Ecology* **32**, 492–501.
- GNASPINI, P. & TRAJANO, E. (2000). Guano communities in tropical caves. In *Subterranean Ecosystems* (eds H. Wilkens, D.C. Culver and W.F. Humphreys), pp 251–268. Elsevier, New York.
- *GONZALEZ-JAUREGUI, M., VALDESPINO, C., SALAME-MÉNDEZ, A., AGUIRRE-LEÓN, G. & RENDÓN-VONOSTEN, J. (2012). Persistent organic contaminants and steroid hormones levels in Morelet's crocodiles from the southern Gulf of Mexico. *Archives of Environmental Contamination and Toxicology* **62**, 445–454.
- GORZULA, S. (1987). The management of crocodylians in Venezuela. *Wildlife management: crocodiles and alligators*, 91–101.
- GOYMER, P. (2018). Editorial: predators on top. *Nature Ecology & Evolution* **2**, 199–199.
- GRADY, J. M., MAITNER, B. S., WINTER, A. S., KASCHNER, K., TITTENSOR, D. P., RECORD, S., SMITH, F. A., WILSON, A. M., DELL, A. I. & ZARNETSKY, P. L. (2019). Metabolic asymmetry and the global diversity of marine predators. *Science* **363**, eaat4220.
- GRANT, P. B. C., LEWIS, T. R., LADUKE, T. C. & RYALL, C. (2008). *Caiman crocodilus* opportunistic foraging. *Herpetological Review* **39**, 345–346.
- GRIGG, G. & KIRSHNER, D. (2015). *Biology and Evolution of Crocodylians*. CSIRO Publishing, Clayton, Australia.
- *GRIGG, G. C., BEARD, L. A., MOULTON, T., OUEIROLO MELO, M. T. & TAPLIN, L. E. (1998). Osmoregulation by the broad-snouted caiman, *Caiman latirostris*, in estuarine habitat in southern Brazil. *Journal of Comparative Physiology - B Biochemical, Systemic, and Environmental Physiology* **168**, 445–452.
- GROOMBRIDGE, B. (1987). The distribution and status of world crocodylians. *Wildlife management: crocodiles and alligators*, 9–21.
- *GUILLETTE, L. J. & EDWARDS, T. M. (2008). Environmental influences on fertility: can we learn lessons from studies of wildlife? *Fertility and Sterility* **89**, 21–24.
- *GUILLETTE, L. J. & GUNDERSON, M. P. (2001). Alteration in development of reproductive and endocrine systems of wildlife populations exposed to endocrine-disrupting contaminants. *Reproduction* **122**, 857–864.
- GUILLETTE, L. J. JR., GROSS, T. S., MASSON, G. R., MATTER, J. M., PERCIVAL, H. F. & WOODWARD, A. R. (1994). Developmental abnormalities of the gonad and abnormal sex hormone concentrations in juvenile alligators from contaminated and control lakes in Florida. *Environmental Health Perspectives* **102**, 680–688.
- *GUILLETTE, L. J. JR., CRAIN, D. A., GUNDERSON, M. P., KOOLS, S. A. E., MILNES, M. R., ORLANDO, E. F., ROONEY, A. A. & WOODWARD, A. R. (2000). Alligators and

- endocrine disrupting contaminants: a current perspective. *American Zoologist* **40**, 438–452.
- *GUNDERSON, L.H. (1994). Vegetation of the Everglades: determinants of community composition. Everglades: the ecosystem and its restoration, 323–340.
- *GUNDERSON, M. P., PICKETT, M. A., MARTIN, J. T., HULSE, E. J., SMITH, S. S., SMITH, L. A., CAMPBELL, R. M., LOWERS, R. H., BOGGS, A. S. P. & GUILLETTE, L. J. (2016). Variations in hepatic biomarkers in American alligators (*Alligator mississippiensis*) from three sites in Florida, USA. *Chemosphere* **155**, 180–187.
- HAEMIG, P. D. (2001). Symbiotic nesting of birds with formidable animals: a review with applications to biodiversity conservation. *Biodiversity and Conservation* **10**, 527–540.
- HALL, P. M. & JOHNSON, D. R. (1987). Nesting biology of *Crocodylus novaeguineae* in Lake Murray District, Papua New Guinea. *Herpetologica* **43**, 249–258.
- HALL, P. M. & MEIER, A. J. (1993). Reproduction and behavior of western mud snakes (*Farancia abacura reinwardtii*) in American alligator nests. *Copeia* **1993**, 219–222.
- HAMMERSCHLAG, N., SCHMITZ, O. J., FLECKER, A. S., LAFFERTY, K. D., SIH, A., ATWOOD, T. B., GALLAGHER, A. J., IRSCHICK, D. J., SKUBEL, R. & COOKE, S. J. (2019). Ecosystem function and services of aquatic predators in the Anthropocene. *Trends in Ecology & Evolution* **34**, 369–383.
- HANSON, J. O., SALISBURY, S. W., CAMPBELL, H. A., DWYER, R. G., JARDINE, T. D. & FRANKLIN, C. E. (2015). Feeding across the food web: the interaction between diet, movement and body size in estuarine crocodiles (*Crocodylus porosus*). *Austral Ecology* **40**, 275–286.
- *HARPER, F. (1930). Alligators of the Okefinokee. *The Scientific Monthly* **1930**, 51–67.
- HAYESODUM, L. A. & JONES, D. (1993). Effects of drought on American alligators (*Alligator mississippiensis*) in Texas. *Texas Journal of Science* **45**, 182–185.
- HEITHAUS, M. R., FRID, A., WIRSING, A. J. & WORM, B. (2008a). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution* **23**, 202–210.
- *HEITHAUS, M. R., WIRSING, A. J., THOMSON, J. A. & BURKHOLDER, D. A. (2008b). A review of lethal and non-lethal effects of predators on adult marine turtles. *Journal of Experimental Marine Biology and Ecology* **356**, 43–51.
- HEITHAUS, M., FRID, A., VAUDO, J., WORM, B. & WIRSING, A. J. (2010). Unraveling the ecological importance of elasmobranchs. In *Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation* (eds J. C. CARRIER, J. A. MUSICK and M. R. HEITHAUS). CRC Press, Boca Raton, FL.
- *HINMAN, B. (2015). *Keystone Species that Live in Ponds, Streams, and Wetlands*. Mitchell Lane Publishers, Inc., Hockessin, DE.
- HOFFMAN, W., BANGROFT, G. T. & SAWICKI, R. J. (1994). Foraging habitat of wading birds in the Water Conservation Areas of the Everglades. Everglades: the ecosystem and its restoration. *St. Lucie Press, Delray Beach, Florida, USA*, 585–614.
- HOOGSTEIJN, R. & CHAPMAN, C. A. (1997). Large ranches as conservation tools in the Venezuelan llanos. *Oryx* **31**, 274–284.
- *HORAI, S., ITAI, T., NOGUCHI, T., YASUDA, Y., ADACHI, H., HYOBU, Y., RYADI, A. S., BOGGS, A. S. P., LOWERS, R., GUILLETTE, L. J. & TANABE, S. (2014). Concentrations of trace elements in American alligators (*Alligator mississippiensis*) from Florida, USA. *Chemosphere* **108**, 159–167.
- *HUNT, R. H. & OGDEN, J. J. (1991). Selected aspects of the nesting ecology of American alligators in the Okefenokee Swamp. *Journal of Herpetology* **25**, 448–453.
- HUTTON, J. M. (1987). Growth and feeding ecology of the Nile crocodile *Crocodylus niloticus* at Ngezi, Zimbabwe. *Journal of Animal Ecology* **56**, 25–38.
- *HUTTON, J. (1989). Movements, home range, dispersal and the separation of size classes in Nile crocodiles. *Integrative and Comparative Biology* **29**, 1033–1049.
- IUCN (2017). The IUCN red list of threatened species. Version 2017–3. Electronic file available at <http://www.iucnredlist.org>. Downloaded on 5 April 2018.
- JACKSON, J. F., CAMPBELL, H. W. & CAMPBELL, K. E. (1974). The feeding habits of crocodylians: validity of the evidence from stomach contents. *Journal of Herpetology* **8**, 378–381.
- *JEFFERY, B.M. & CHERKISS, M.S. (2012). Annual assessment update for comprehensive Everglades Restoration Plan (CERP): American alligator density, size, and hole occupancy and American crocodile juvenile growth & survival. Prepared for U.S. Army Corps of Engineers, Jacksonville, FL.
- *JEFFREE, R. A., MARKICH, S. J. & TUCKER, A. D. (2005). Patterns of metal accumulation in osteoderms of the Australian freshwater crocodile, *Crocodylus johnstoni*. *Science of the Total Environment* **336**, 71–80.
- *JOANEN, T., MCNEASE, L., ELSEY, R. & STATON, M. (1997). The commercial consumptive use of the American alligator (*Alligator mississippiensis*) in Louisiana, its effects on conservation. In *Harvesting Wild Species—Implications for Biodiversity* (ed. C. H. FREESE), pp. 465–506. The Johns Hopkins University Press, Baltimore.
- JONES, C. G., LAWTON, J. H. & SHACHAK, M. (1994). Organisms as ecosystem engineers. In *Ecosystem Management* (eds F. B. SAMSON and F. L. KNOPP), pp. 130–147. Springer, New York.
- JONSSON, B. & JONSSON, N. (2003). Migratory Atlantic salmon as vectors for the transfer of energy and nutrients between freshwater and marine environments. *Freshwater Biology* **48**, 21–27.
- *JOUBERT, S. & VAN GOGH, J. (2007). *The Kruger National Park: A History*. High Branching (Pty), Johannesburg, South Africa.
- KAY, W. R. (2004). Movements and home ranges of radio-tracked *Crocodylus porosus* in the Cambridge Gulf region of Western Australia. *Wildlife Research* **31**, 495–508.
- *KEDDY, P. A., CAMPBELL, D., MCFALLS, T., SHAFFER, G. P., MOREAU, R., DRANGUET, C. & HELENIAK, R. (2007). The wetlands of lakes Pontchartrain and Maurepas: past, present and future. *Environmental Reviews* **15**, 43–77.
- KEDDY, P., GOUGH, L., NYMAN, J. A., MCFALLS, T., CARTER, J. & SIEGRIST, J. (2009). Alligator hunters, pelt traders, and runaway consumption of gulf coast marshes. In *Human Impacts on Salt Marshes: A Global Perspective* (eds B. SILLIMAN, E. D. GROSHOLZ and M. D. BERTNESS), pp. 115–133. University of California Press, Berkeley, CA.
- *KELLOGG, A. R. (1929). Habits and economic importance of alligators. *US Department of Agriculture Technical Bulletin* **147**.
- *KHAN, B. & TANSEL, B. (2000). Mercury bioconcentration factors in American alligators (*Alligator mississippiensis*) in the Florida Everglades. *Ecotoxicology and Environmental Safety* **47**, 54–58.
- *KLEMENS, M. W. & THORBARNARSON, J. B. (1995). Reptiles as a food resource. *Biodiversity and Conservation* **4**, 281–298.
- *KOFRON, C. P. (1989). Nesting ecology of the Nile crocodile (*Crocodylus niloticus*). *African Journal of Ecology* **27**, 335–341.
- *KOFRON, C. P. (1993). Behavior of Nile crocodiles in a seasonal river in Zimbabwe. *Copeia* **1993**, 463–469.
- VAN DE KOPPEL, J., VAN DER HEIDE, T., ALTIERI, A. H., ERIKSSON, B. K., BOUMA, T. J., OLFF, H. & SILLIMAN, B. R. (2015). Long-distance interactions regulate the structure and resilience of coastal ecosystems. *Annual Review of Marine Science* **7**, 139–158.
- KUNDZEWICZ, Z., MATA, L., ARNELL, N. W., DÖLL, P., JIMENEZ, B., MILLER, K., OKI, T., SEN, Z. & SHIKLOMANOV, I. (2008). The implications of projected climate change for freshwater resources and their management. *Hydrological Sciences Journal* **53**, 3–10.
- KUSHLAN, J. A. (1974). Observations on the role of the American alligator (*Alligator mississippiensis*) in the southern Florida wetlands. *Copeia* **1974**, 993–996.
- KUSHLAN, J. A. & KUSHLAN, M. S. (1980). Everglades alligator nests: nesting sites for marsh reptiles. *Copeia* **1980**, 930–932.
- KUSHLAN, J. A. & MAZZOTTI, F. J. (1989). Population biology of the American crocodile. *Journal of Herpetology* **23**, 7–21.
- LANCE, V. A. (2003). Alligator physiology and life history: the importance of temperature. *Experimental Gerontology* **38**, 801–805.
- *LANCE, V. A., ELSEY, R. M., TROSCLAIR, P. L. & NUNEZ, L. A. (2011). Long-distance movement by American alligators in Southwest Louisiana. *Southeastern Naturalist* **10**, 389–398.
- LANG, J. W. (1987). Crocodylian behaviour: implications for management. *Wildlife management: crocodiles and alligators*, 273–294.
- *LANHUPUY, W. (1987). Australian aboriginal attitudes to crocodile management. *Wildlife Management: Crocodile and Alligators*, 145–147.
- *LARRIERA, A. & PINA, C. I. (2000). *Caiman latirostris* (Broad-snouted Caiman) nest predation: does low rainfall facilitate predator access? *Herpetological Natural History* **7**, 73–77.
- *LATORRE, M. A., ROMITO, M. L., LARRIERA, A., POLETTA, G. L. & SIROSKI, P. A. (2016). Total and differential white blood cell counts in *Caiman latirostris* after in ovo and in vivo exposure to insecticides. *Journal of Immunotoxicology* **13**, 903–908.
- LAWLER, J. J., AUKEMA, J. E., GRANT, J. B., HALPERN, B. S., KAREIVA, P., NELSON, C. R., OHLETH, K., OLDEN, J. D., SCHLAEPFER, M. A. & SILLIMAN, B. R. (2006). Conservation science: a 20-year report card. *Frontiers in Ecology and the Environment* **4**, 473–480.
- 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.
- *LETNIC, M., WEBB, J. K. & SHINE, R. (2008). Invasive cane toads (*Bufo marinus*) cause mass mortality of freshwater crocodiles (*Crocodylus johnstoni*) in tropical Australia. *Biological Conservation* **141**, 1773–1782.
- LEVI, T. & WILMERS, C. C. (2012). Wolves–coyotes–foxes: a cascade among carnivores. *Ecology* **93**, 921–929.
- *LINDSEY, P. A., ROULET, P. & ROMANACH, S. (2007). Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation* **134**, 455–469.
- LOFTUS, W. F. & EKLUND, A.-M. (1994). Long-term dynamics of an Everglades small-fish assemblage. *Everglades: the ecosystem and its restoration*. *St. Lucie Press, Delray Beach, Florida*, 461–483.
- *LOVELESS, C. M. (1959). A study of the vegetation in the Florida Everglades. *Ecology* **40**, 1–9.
- LUISELLI, L., AKANI, G. & CAPIZZI, D. (1999). Is there any interspecific competition between dwarf crocodiles (*Osteoleaemus tetraspis*) and Nile monitors (*Varanus niloticus ornatus*) in the swamps of central Africa? A study from south-eastern Nigeria. *Journal of Zoology* **247**, 127–131.
- MAFFEI, F. & DA SILVEIRA, R. (2013). First record of multiple nests of yellow-spotted river turtle (*Podocnemis unifilis*) in a nest of black caiman (*Melanosuchus niger*) in Amazonia. *Boletim do Museu Paraense Emílio Goeldi Ciências Naturais* **8**, 461–465.
- *MAGNUSSON, W. E. (1980). Habitat required for nesting by *Crocodylus porosus* (Reptilia: Crocodylidae) in northern Australia. *Journal of Wildlife Research* **7**, 149–156.

- MAGNUSSON, W. E. (1985). Habitat selection, parasites and injuries in Amazonian crocodylians. *Amazonia* **9**, 193–204.
- MAGNUSSON, W. E. (1990). Crocodiles by Rodney steel. *Copeia* **1990**, 1185–1204.
- MAGNUSSON, W. E. & LIMA, A. P. (1991). The ecology of a cryptic predator, *Paleosuchus trigonatus*, in a tropical rainforest. *Journal of Herpetology* **25**, 41–48.
- MAGNUSSON, W. E. & TAYLOR, J. A. (1982). Wallows of *Crocodylus porosus* as dry season refuges in swamps. *Copeia* **2**, 478–480.
- *MAGNUSSON, W. E., DA SILVA, E. V. & LIMA, A. P. (1987). Diets of Amazonian crocodylians. *Journal of Herpetology* **21**, 85.
- *MAGNUSSON, W. E., LIMA, A. P., HERO, J.-M., SANIOTTI, T. M. & YAMAKOSHI, M. (1990). *Paleosuchus trigonatus* nests: sources of heat and embryo sex ratios. *Journal of Herpetology* **24**, 397–400.
- *MANALO, R. I. & ALCALA, A. C. (2015). Conservation of the Philippine crocodile *Crocodylus mindorensis* (Schmidt 1935): in situ and ex situ measures. *International Zoo Yearbook* **49**, 113–124.
- MANOLIS, S., WEBB, G. & BRITTON, A. (2002). Crocodylians and other reptiles: bioindicators of pollution. In *The Finnis River. A Natural Laboratory of Mining Impact- Past, Present and Future* (eds S. J. MARKICH and R. A. JEFFREE), pp. 65–69. Australian Nuclear Science and Technology Organisation (ANSTO), Clayton, Australia.
- *MARCÓ, M. V. P., LARRIERA, A. & PIÑA, C. I. (2015). Red fire ants (*Solenopsis invicta*) effects on broad-snouted caiman (*Caiman latirostris*) nest success. *Journal of Herpetology* **49**, 70–74.
- *MARKICH, S. J., JEFFREE, R. A. & HARCH, B. D. (2002). Catchment-specific element signatures in estuarine crocodiles (*Crocodylus porosus*) from the Alligator Rivers Region, northern Australia. *Science of the Total Environment* **287**, 83–95.
- MARTIN, S. (2008). Global diversity of crocodiles (Crocodylia, Reptilia) in freshwater. *Hydrobiologia* **595**, 587–591.
- MARTIN, A. J. (2017). *The Evolution Underground: Burrows, Bunkers, and the Marvelous Subterranean World Beneath our Feet*. Pegasus Books, Cambridge, UK.
- MARTIN, T. W. & HIGHT, A. R. (1977). *Alligator food habits and their relationship to Everglade kite habitat productivity*. U.S. Fish and Wildlife Service. (Unpublished Report).
- *MAZZOTTI, F. J. (1989). Factors affecting the nesting success of the American crocodile, *Crocodylus acutus*, in Florida Bay. *Bulletin of Marine Science* **44**, 220–228.
- MAZZOTTI, F. J. & BRANDT, L. A. (1994). Ecology of the American alligator in a seasonally fluctuating environment. In *Everglades: The Ecosystem and its Restoration* (eds S. DAVIS and J. OGDEN), pp. 485–505. St Lucie Press, Delray Beach, FL.
- MAZZOTTI, F. & BRANDT, L. (1995). A biological assessment of the C-111 Project on the American Crocodile in northeastern Florida Bay, *Everglades National Park*. US Department of the Interior, National Park Service, Everglades National Park, Homestead, Florida.
- MAZZOTTI, F. J., CHERKISS, M., COOK, G. & MCKERCHER, E. (2003). Status and conservation of the American crocodile in Florida: Recovering an endangered species while restoring an endangered ecosystem. University of Florida, FL.
- 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.
- 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.
- *MAZZOTTI, F. J., CHERKISS, M. S., BRANDT, L. A., FUJISAKI, I., HART, K., JEFFERY, B., MCMURRY, S. T., PLATT, S. G., RAINWATER, T. R. & VINCI, J. (2012). Body condition of Morelet's crocodiles (*Crocodylus moreletii*) from Northern Belize. *Journal of Herpetology* **46**, 356–362.
- MAZZOTTI, F. J., MCEACHERN, M., ROCHFORD, M., REED, R. N., ECKLES, J. K., VINCI, J., EDWARDS, J. & WASILEWSKI, J. (2015). *Tupinambis merianae* as nest predators of crocodylians and turtles in Florida, USA. *Biological Invasions* **17**, 47–50.
- *MCCAULEY, D. J. (2006). Selling out on nature. *Nature* **443**, 27.
- *MCLHENNY, E. A. (1935). *The alligator's Life History*. The Christopher Publishing House, Boston, MA.
- MCNEELY, J. A. & SOGHACZEWSKI, P. S. (1991). *Soul of the Tiger: Searching for nature's Answers in Southeast Asia*. University of Hawaii Press, Honolulu.
- *MEDEM, F. (1981). *Los crocodylia de Sur America, Volume 1, Los Crocodylia de Colombia*. Colciencias, Colombia.
- MELSTROM, K. M. & IRMI, R. B. (2019). Repeated evolution of herbivorous Crocodyliforms during the age of dinosaurs. *Current Biology* **29**, 2389–2395.e3.
- MERCHANT, M., MURRAY, C. M. & COOPER, A. (2014). American alligator nests as microhabitat for a diversity of vertebrates. *Herpetological Review* **45**, 201–203.
- *DE MIRANDA, E. B. P. (2017). The plight of reptiles as ecological actors in the tropics. *Frontiers in Ecology and Evolution* **5**, 159.
- MIRANDA, E. B. D. (2017). The plight of reptiles as ecological actors in the tropics. *Frontiers in Ecology and Evolution* **5**, 159.
- MITCHELL, M. S. & POWELL, R. A. (2003). Response of black bears to forest management in the southern Appalachian Mountains. *The Journal of Wildlife Management* **67**, 692–705.
- MITCHELL, M. G., BENNETT, E. M. & GONZALEZ, A. (2013). Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. *Ecosystems* **16**, 894–908.
- *MOBARAKI, A. (2002). Snub-nosed crocodile (*Crocodylus palustris*) study in Iran. In *Proceedings of the 16th Working Meeting of the IUCN/SSC Crocodile Specialist Group*, pp. 253–256. IUCN, Gland, Switzerland.
- *MOBARAKI, A. & ABTIN, E. (2007). Movement behavior of muggers, a potential threat. *Crocodile Specialist Group Newsletter* **26**, 4.
- *MODHA, M. L. (1967). The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. *African Journal of Ecology* **5**, 74–95.
- *MODHA, M. L. (1968). Crocodile research project, Central Island, Lake Rudolf: 1967 breeding season. *African Journal of Ecology* **6**, 148–150.
- *MOISER, C. M. & BARBER, A. D. (1994). The crocodile pools of the Western Division, The Gambia. *British Herpetological Society Bulletin* **47**, 16–22.
- MONROE, R. & GARRETT, R. (1979). *Chelombia testudinaria* (L.) (Cirripedia, Coronulidae) on *Crocodylus porosus* Schneider, a new host record. *Crustaceana* **36**, 108–108.
- *MONTINI, J. P., PIÑA, C. I., LARRIERA, A., SIROSKI, P. & VERDADE, L. M. (2006). The relationship between nesting habitat and hatching success in *Caiman latirostris* Crocodylia, Alligatoridae. *Phyllomedusa* **5**, 91–96.
- MOURO, G., COUTINHO, M., MAURO, R., CAMPOS, Z., TOMÁS, W. & MAGNUSSON, W. (2000). Aerial surveys of caiman, marsh deer and pampas deer in the Pantanal Wetland of Brazil. *Biological Conservation* **92**, 175–183.
- MYERS, R. A., BAUM, J. K., SHEPHERD, T. D., POWERS, S. P. & PETERSON, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**, 1846–1850.
- NAIR, T. & KRISHNA, Y. C. (2013). Vertebrate fauna of the Chambal River basin, with emphasis on the National Chambal Sanctuary, India. *Journal of Threatened Taxa* **5**, 3620–3641.
- NELL, L. A. (2014). Exploring benefits to American alligators (*Alligator mississippiensis*) associating with long-legged wading bird nesting colonies in the Everglades. MSc Thesis, University of Florida.
- NELL, L. A. & FREDERICK, P. C. (2015). Fallen nestlings and regurgitant as mechanisms of nutrient transfer from nesting wading birds to crocodylians. *Wetlands* **35**, 723–732.
- *NELL, L. A., FREDERICK, P. C., MAZZOTTI, F. J., VLIET, K. A. & BRANDT, L. A. (2016). Presence of breeding birds improves body condition for a crocodylian nest protector. *PLoS One* **11**, e0149572.
- *NIFONG, J. C. (2016). Living on the edge: trophic ecology of *Alligator mississippiensis* (American alligator) with access to a shallow estuarine impoundment. *Bulletin of the Florida Museum of Natural History* **54**, 13–49.
- *NIFONG, J. C. & FRICK, M. G. (2011). First record of the american alligator (*Alligator mississippiensis*) as a host to the sea turtle barnacle (*Chelombia testudinaria*). *Southeastern Naturalist* **10**, 557–560.
- *NIFONG, J. C. & LOWERS, R. H. (2017). Reciprocal intraguild predation between American alligators, *Alligator mississippiensis*, and Elasmobranchii in the southeastern United States. *Southeastern Naturalist* **16**, 383–396.
- *NIFONG, J. C. & SILLIMAN, B. R. (2013). Impacts of a large-bodied, apex predator (*Alligator mississippiensis* Daudin 1801) on salt marsh food webs. *Journal of Experimental Marine Biology and Ecology* **440**, 185–191.
- NIFONG, J. C. & SILLIMAN, B. (2017). Abiotic factors influence the dynamics of marine habitat use by a highly mobile “freshwater” top predator. *Hydrobiologia* **802**, 155–174.
- *NIFONG, J. C., FRICK, M. G. & EASTMAN, S. F. (2011). Putative predation and scavenging of two sea turtle species by the American alligator, *Alligator mississippiensis*, in coastal southeastern United States. *Herpetological Review* **42**, 511–513.
- NIFONG, J. C., ROSENBLATT, A. E., JOHNSON, N. A., BARICHVICH, W., SILLIMAN, B. R. & HEITHAUS, M. R. (2012). American alligator digestion rate of blue crabs and its implications for stomach contents analysis. *Copeia* **2012**, 419–423.
- NIFONG, J. C., NIFONG, R. L., SILLIMAN, B. R., LOWERS, R. H., GUILLETTE, L. J. JR., FERGUSON, J. M., WELSH, M., ABERNATHY, K. & MARSHALL, G. (2014). Animal-borne imaging reveals novel insights into the foraging behaviors and diel activity of a large-bodied apex predator, the American alligator (*Alligator mississippiensis*). *PLoS One* **9**, e83953.
- *NIFONG, J. C., LAYMAN, C. A. & SILLIMAN, B. R. (2015). Size, sex and individual-level behaviour drive intrapopulation variation in cross-ecosystem foraging of a top-predator. *Journal of Animal Ecology* **84**, 35–48.
- *NILSEN, F. M., DORSEY, J. E., LOWERS, R. H., GUILLETTE, L. J., LONG, S. E., BOWDEN, J. A. & SCHOCK, T. B. (2017). Evaluating mercury concentrations and body condition in American alligators (*Alligator mississippiensis*) at Merritt Island National Wildlife Refuge (MINWR), Florida. *Science of the Total Environment* **607–608**, 1056–1064.
- *OGDEN, J. C. (2005). Everglades ridge and slough conceptual ecological model. *Wetlands* **25**, 810–820.
- *OGDEN, J. C., DAVIS, S. M., JACOBS, K. J., BARNES, T. & FLING, H. E. (2005). The use of conceptual ecological models to guide ecosystem restoration in South Florida. *Wetlands* **25**, 795–809.

- *OLUPONA, J. K. (1993). Some notes on animal symbolism in African religion and culture. *Anthropology and Humanism* **18**, 3–12.
- ORDIZ, A., BISCHOF, R. & SWENSON, J. E. (2013). Saving large carnivores, but losing the apex predator? *Biological Conservation* **168**, 128–133.
- ORMEROD, S., DOBSON, M., HILDREW, A. & TOWNSEND, C. (2010). Multiple stressors in freshwater ecosystems. *Freshwater Biology* **55**, 1–4.
- *ORTIZ, R. M., PLOTKIN, P. T. & OWENS, D. W. (1997). Predation upon olive ridley sea turtles (*Lepidochelys olivacea*) by the American crocodile (*Crocodylus acutus*) at playa Nancite, Costa Rica. *Chelonian Conservation and Biology* **2**, 585–587.
- OUBOTER, P. E. (1996). *Ecological Studies on Crocodylians in Suriname: Niche Segregation and Competition in Three Predators*. SPB Academic Publishing, Amsterdam, The Netherlands.
- *OUBOTER, P. E. & NANHOE, L. M. (1987). Notes on nesting and parental care in *Caiman crocodylus crocodylus* in northern Suriname and an analysis of crocodylian nesting habitats. *Amphibia-Reptilia* **8**, 331–347.
- *OUBOTER, P. E. & NANHOE, 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.
- OUY, S., HOR, L., SAM, H., SONN, P., SIMPSON, B. & DALTRY, J. (2009). A comparative study of incentive-based schemes for Siamese crocodile *Crocodylus siamensis* conservation in the Cardamom Mountains, Cambodia. *Cambodian Journal of Natural History* **2009**, 40–57.
- *PALIS, J. G. (1989). *Alligator mississippiensis* (American alligator). Foraging behavior. *Herpetological Review* **20**, 69.
- PALMER, M. L. & MAZZOTTI, F. J. (2004). Structure of everglades alligator holes. *Wetlands* **24**, 115–122.
- PAOLILLO, O. A. & GORZULA, S. (1985). *Palaosuchus palpebrosus* (dwarf caiman). Migration. *Herpetological Review* **16**, 27.
- *PARRY, L., BARLOW, J. & PEREIRA, H. (2014). Wildlife harvest and consumption in Amazonia's urbanized wilderness. *Conservation Letters* **7**, 565–574.
- *PASSARIELLO, P. (1999). Me and my totem: cross-cultural attitudes towards animals. Attitudes to animals: Views in animal welfare, 12–25.
- PAUWELS, O., BARR, B. & SANCHEZ, M. (2007). Diet and size records for *Crocodylus cataphractus* (Crocodylidae) in South-Western Gabon. *Hamadryad* **31**, 360.
- *PEARSON, R. G. (2016). Reasons to conserve nature. *Trends in Ecology & Evolution* **31**, 366–371.
- *PEPPER, C. B., RAINWATER, T. R., PLATT, S. G., DEVER, J. A., ANDERSON, T. A. & MCMURRY, S. T. (2004). Organochlorine pesticides in chloroalloantoic membranes of Morelet's crocodile eggs from Belize. *Journal of Wildlife Diseases* **40**, 493–500.
- PEREIRA, H. M., LEADLEY, P. W., PROENÇA, V., ALKEMADE, R., SCHARLEMANN, J. P., FERNANDEZ-MANJARRÉS, J. F., ARAÚJO, M. B., BALVANERA, P., BIGGS, R. & CHEUNG, W. W. (2010). Scenarios for global biodiversity in the 21st century. *Science* **330**, 1496–1501.
- *PÉREZ-HIGAREDA, G., RANGEL-RANGEL, A., SMITH, H. M. & CHISZAR, D. (1989). Comments on the food and feeding habits of Morelet's crocodile. *Copeia* **1989**, 1039–1041.
- *PHELPS, R. J., FOCARDI, S., FOSSI, C., LEONZIO, C. & RENZONI, A. (1986). Chlorinated hydrocarbons and heavy metals in crocodile eggs from Zimbabwe. *Transactions of the Zimbabwe Scientific Association* **63**, 8–15.
- *PHELPS, R. J., TOET, M. & HUTTON, J. M. (1989). DDT residues in the fat of crocodiles from Lake Kariba, Zimbabwe. *Transactions of the Zimbabwe Scientific Association* **64**, 9–14.
- *PINTOR, L. M. & SOLUK, D. A. (2006). Evaluating the non-consumptive, positive effects of a predator in the persistence of an endangered species. *Biological Conservation* **130**, 584–591.
- *PLATT, S. G. & THORBJARNARSON, J. B. (2000). Status and conservation of the American crocodile, *Crocodylus acutus*, in Belize. *Biological Conservation* **96**, 13–20.
- *PLATT, S. G., RAINWATER, T. R., FINGER, A. G., THORBJARNARSON, J. B., ANDERSON, T. A. & MCMURRY, S. T. (2006a). Food habits, ontogenetic dietary partitioning and observations of foraging behaviour of Morelet's crocodile (*Crocodylus moreletii*) in northern Belize. *Herpetological Journal* **16**, 281–290.
- *PLATT, S. G., SOVANNARA, H., KHENG, L., STUART, B. L. & WALSTON, J. (2006b). *Crocodylus siamensis* along the Sre Ambel river, southern Cambodia: habitat, nesting, and conservation. *Herpetological Natural History* **9**, 183–188.
- *PLATT, S. G., RAINWATER, T. R., SNIDER, S., GAREL, A., ANDERSON, T. A. & MCMURRY, S. T. (2007). Consumption of large mammals by *Crocodylus moreletii*: field observations of necrophagy and interspecific kleptoparasitism. *The Southwestern Naturalist* **52**, 310–317.
- *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.
- *PLATT, S. G., MONYRATH, V., SOVANNARA, H., KHENG, L. & RAINWATER, T. R. (2012). Nesting phenology and clutch characteristics of captive Siamese crocodiles (*Crocodylus siamensis*) in Cambodia. *Zoo Biology* **31**, 534–545.
- PLATT, S. G., THORBJARNARSON, J. B., RAINWATER, T. R. & MARTIN, D. R. (2013). Diet of the American crocodile (*Crocodylus acutus*) in marine environments of coastal Belize. *Journal of Herpetology* **47**, 1–10.
- *PLATT, S. G., THONGSAVATH, O., OUTHANEKONE, P. & RAINWATER, T. R. (2018). Notes on traditional ecological knowledge and ethnoherpetology of Siamese crocodiles in Lao, PDR. *Crocodyle Specialist Group Newsletter* **37**, 6–12.
- VAN DER PLOEG, J., CAULLAN-CUREG, M., VAN WEERD, M. & DE GROOT, W. T. (2011a). Assessing the effectiveness of environmental education: mobilizing public support for Philippine crocodile conservation. *Conservation Letters* **4**, 313–323.
- VAN DER PLOEG, J., CAULLAN-CUREG, M., VAN WEERD, M. & PERSOON, G. (2011b). 'Why must we protect crocodiles?' Explaining the value of the Philippine crocodile to rural communities. *Journal of Integrative Environmental Sciences* **8**, 287–298.
- VAN DER PLOEG, J., RATU, F., VIRAVIRA, J., BRIEN, M., WOOD, C., ZAMA, M., GOMESE, C. & HURUTARAU, J. (2019). *Human-crocodile conflict in Solomon Islands*. Penang, Malaysia: WorldFish. Program Report: 2019-02.
- *POE, S. (1996). Data set incongruence and the phylogeny of crocodylians. *Systematic Biology* **45**, 393–414.
- POLETTA, G., LARRIERA, A., KLEINSORGE, E. & MUDRY, M. (2008). *Caiman latirostris* (broad-snouted caiman) as a sentinel organism for genotoxic monitoring: basal values determination of micronucleus and comet assay. *Mutation Research/Genetic Toxicology and Environmental Mutagenesis* **650**, 202–209.
- *POLETTA, G. L., LARRIERA, A., KLEINSORGE, E. & MUDRY, M. D. (2009). Genotoxicity of the herbicide formulation Roundup® (glyphosate) in broad-snouted caiman (*Caiman latirostris*) evidenced by the Comet assay and the Micronucleus test. *Mutation Research - Genetic Toxicology and Environmental Mutagenesis* **672**, 95–102.
- POLIS, G. A., ANDERSON, W. B. & HOLT, R. D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**, 289–316.
- PONGSIRI, M. J., ROMAN, J., EZENWA, V. O., GOLDBERG, T. L., KOREN, H. S., NEWBOLD, S. C., OSTFELD, R. S., PATTANAYAK, S. K. & SALKELD, D. J. (2009). Biodiversity loss affects global disease ecology. *Bioscience* **59**, 945–954.
- *POOLEY, A. C. (1969). Preliminary studies on the breeding of the Nile crocodile *Crocodylus niloticus* in Zululand. *Lammergeyer* **10**, 22–44.
- *POOLEY, A. C. (1973). Conservation and management of crocodiles in Africa. *South African Journal of Wildlife Research* **3**, 101–103.
- POOLEY, A. (1989). Food and feeding habits. In *Crocodyles and alligators*, pp. 76–91.
- POST, W. & SEALS, C. A. (1991). Bird density and productivity in an impounded Cattail marsh. *Journal of Field Ornithology* **62**, 195–199.
- POWER, M. E. (1984). Depth distributions of armored catfish: predator-induced resource avoidance? *Ecology* **65**, 523–528.
- POWER, M. E., TILMAN, D., ESTES, J. A., MENGE, B. A., BOND, W. J., MILLS, L. S., DAILY, G., CASTILLA, J. C., LUBCHENCO, J. & PAINE, R. T. (1996). Challenges in the quest for keystones. *Bioscience* **46**, 609–620.
- *DU PREEZ, M., GOVENDER, D., KYLIN, H. & BOUWMAN, H. (2018). Metallic elements in Nile Crocodile eggs from the Kruger National Park, South Africa. *Ecotoxicology and Environmental Safety* **148**, 930–941. Elsevier Inc.
- PRINGLE, R. M. (2017). How large herbivores subsidize aquatic food webs in African savannas. *Proceedings of the National Academy of Sciences* **114**, 7489–7491.
- PRUGH, L. R., STONER, C. J., EPPS, C. W., BEAN, W. T., RIPLEY, W. J., LALIBERTE, A. S. & BRASHARES, J. S. (2009). The rise of the mesopredator. *Bioscience* **59**, 779–791.
- QUEENSLAND GOVERNMENT (1995). *Crocodyles*. The State of Queensland, Australia. Electronic file available at <https://www.qld.gov.au/environment/plants-animals/animals/crocodyles> Accessed 13.09.2018
- RADLOFF, F. G. T., HOBSON, K. A. & LESLIE, A. J. (2012). Characterising ontogenetic niche shifts in Nile crocodile using stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analyses of scute keratin. *Isotopes in Environmental and Health Studies* **48**, 439–456.
- *RAINWATER, T. R., ADAIR, B. M., PLATT, S. G., ANDERSON, T. A., COBB, G. P. & MCMURRY, S. T. (2002). Mercury in Morelet's crocodile eggs from northern Belize. *Archives of Environmental Contamination and Toxicology* **42**, 319–324.
- *RAINWATER, T. R., WU, T. H., FINGER, A. G., CAÑAS, J. E., YU, L., REYNOLDS, K. D., COIMBATORE, G., BARR, B., PLATT, S. G., COBB, G. P., ANDERSON, T. A. & MCMURRY, S. T. (2007). Metals and organochlorine pesticides in caudal scutes of crocodiles from Belize and Costa Rica. *Science of the Total Environment* **373**, 146–156.
- RAO, J. R. & SINGH, K. (1993). Communal nesting by gharial *Gavialis gangeticus* (Gmelin) (Reptilia: Crocodylia) in National Chambal Sanctuary. *Journal of Bombay Natural History Society* **90**, 17–22.
- RAY, J. C., REDFORD, K. H., BERGER, J. & STENECK, R. (2005). *Is Large Carnivore Conservation Equivalent to Biodiversity Conservation and How Can we Achieve Both*, pp. 400–427. Large Carnivores and the Conservation of Biodiversity. Island Press, Washington, DC.
- RAY, J., REDFORD, K. H., STENECK, R. & BERGER, J. (2013). *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington, DC.
- READ, M. A., GRIGG, G. C., IRWIN, S. R., SHANAHAN, D. & FRANKLIN, C. E. (2007). Satellite tracking reveals long distance coastal travel and homing by translocated estuarine crocodiles, *Crocodylus porosus*. *PLoS One* **2**, 1–5.

- *REVOL, B. (1995). Crocodile farming and conservation, the example of Zimbabwe. *Biodiversity and Conservation* **4**, 299–305.
- *REY, F., RAMOS, J. G., STOKER, C., BUSSMANN, L. E., LUQUE, E. H. & MUÑOZ-DE-TORO, M. (2006). Vitellogenin detection in *Caiman latirostris* (Crocodylia: Alligatoridae): a tool to assess environmental estrogen exposure in wildlife. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **176**, 243–251.
- *RIBNICK, R. O. (1989). American wildlife in symbol and story. *Western Folklore* **48**, 72–274.
- RICE, K., MAZZOTTI, F. & BRANDT, L. (2005). Status of the American alligator (*Alligator mississippiensis*) in southern Florida and its role in measuring restoration success in the Everglades. In *Status and Conservation of Florida Amphibians and Reptiles*, pp. 145–453. Krieger Publishers, Melbourne.
- RICE, A. N., WOODWARD, J. P. R. A. R., CARBONNEAU, D. A. & PERCIVAL, H. F. (2007a). Alligator diet in relation to alligator mortality on Lake Griffin, FL. *Southeastern Naturalist* **6**, 97–2110.
- RICE, K. G., MAZZOTTI, F. J., JEFFERY, B. M. & PERCIVAL, H. F. (2007b). *American alligator distribution, size, and hole occupancy and American crocodile juvenile growth and survival: Annual Report*. US Army Corps of Engineers, Jacksonville, Jacksonville, FL.
- *RICHARDS, P. M., MOOIJ, W. M. & DEANGELIS, D. L. (2004). Evaluating the effect of salinity on a simulated American crocodile (*Crocodylus acutus*) population with applications to conservation and Everglades restoration. *Ecological Modelling* **180**, 371–394.
- RILEY, J. & HUCHZERMAYER, F. W. (2000). Diet and lung parasites of swamp forest Dwarf Crocodiles (*Osteolaemus tetraspis osborni*) in the Northern Congo Republic. *Copeia* **2000**, 582–586.
- RIPPLE, W. J. & BESCHTA, R. L. (2004). Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* **54**, 755–766.
- RIPPLE, W. J., ESTES, J. A., BESCHTA, R. L., WILMERS, C. C., RITCHIE, E. G., HEBBLEWHITE, M., BERGER, J., ELMHAGEN, B., LETNIC, M. & NELSON, M. P. (2014). Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484.
- RITCHIE, E. G. & JOHNSON, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**, 982–998.
- RITCHIE, E. G., ELMHAGEN, B., GLEN, A. S., LETNIC, M., LUDWIG, G. & McDONALD, R. A. (2012). Ecosystem restoration with teeth: what role for predators? *Trends in Ecology & Evolution* **27**, 265–271.
- *RIVERA, S. J., PACHECO, L. F., ACHÁ, D., MOLINA, C. I. & MIRANDA-CHUMACERO, G. (2016). Low total mercury in *Caiman yacare* (Alligatoridae) as compared to carnivorous, and non-carnivorous fish consumed by Amazonian indigenous communities. *Environmental Pollution* **218**, 366–371.
- ROBINSON, S. K. (1985). Coloniality in the yellow-rumped cacique as a defense against nest predators. *The Auk* **102**, 506–519.
- RÖDDER, D., ENGLER, J. O., BONKE, R., WEINSHEIMER, F. & PERTEL, W. (2010). Fading of the last giants: an assessment of habitat availability of the Sunda gharial *Tomistoma schlegelii* and coverage with protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**, 678–684.
- ROSAS, H. L., LÓPEZ-BARRERA, F., MORENO-CASASOLA, P., AGUIRRE-LEÓN, G., CÁZARES-HERNÁNDEZ, E. & SÁNCHEZ-HIGUEREDO, L. (2010). Indicators of recovery in a tropical freshwater marsh invaded by an African grass. *Ecological Restoration* **28**, 324–332.
- 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.
- ROSENBLATT, A. & NIFONG, J. C. (2018). Understanding alligator feeding patterns: historical and modern perspectives. In *American Alligators: Habitats, Behaviors, and Threats* (eds S. HENKE and C. B. EVERSOLE), pp. 155–174. Nova Science Publishers, New York.
- ROSENBLATT, A. E., HEITHAUS, M. R., MATHER, M. E., MATICH, P., NIFONG, J. C., RIPPLE, W. J. & SILLIMAN, B. R. (2013a). The roles of large top predators in coastal ecosystems new insights from long term ecological research. *Oceanography* **26**, 157–167.
- *ROSENBLATT, A. E., HEITHAUS, M. R., MAZZOTTI, F. J., CHERKISS, M. & JEFFERY, B. M. (2013b). Intra-population variation in activity ranges, diel patterns, movement rates, and habitat use of American alligators in a subtropical estuary. *Estuarine, Coastal and Shelf Science* **135**, 182–190.
- ROSENBLATT, A. E., NIFONG, J. C., HEITHAUS, M. R., MAZZOTTI, F. J., CHERKISS, M. S., JEFFERY, B. M., ELSEY, R. M., DECKER, R. A., SILLIMAN, B. R., GUILLETTE, L. J., LOWERS, R. H. & LARSON, J. C. (2015). Factors affecting individual foraging specialization and temporal diet stability across the range of a large “generalist” apex predator. *Oecologia* **178**, 5–16.
- *SAALFELD, D. T., CONWAY, W. C. & CALKINS, G. E. (2011). Food habits of American alligators (*Alligator mississippiensis*) in East Texas. *Southeastern Naturalist* **10**, 659–672.
- SAH, S. A. M. & STUEBING, R. B. (1996). Diet, growth and movements of juvenile crocodiles *Crocodylus porosus* Schneider in the Klias River, Sabah, Malaysia. *Journal of Tropical Ecology* **12**, 651–662.
- *SAMPAIO, P. R. M., DA SILVA, M. N., DE MATOS, S. A., DE MATOS, L. R. A. & ACOSTA, M. (2013). First report of predation by a caiman (*Paleosuchus trigonatus*, Crocodylia: Alligatoridae) on a caecilian (*Caecilia marcusii*, Gymnophiona: Caeciliidae). *Salamandra* **49**, 227–228.
- SANTOS, S. A., NOGUEIRA, M. S., PINHEIRO, M. S., CAMPOS, Z., MAGNUSSON, W. E. & MOURAO, G. M. (1996). Diets of *Caiman crocodilus yacare* from different habitats in the Brazilian Pantanal. *Herpetological Journal* **6**, 111–117.
- SANTOS, X., NAVARRO, S., CAMPOS, J. C., SANPERA, C. & BRITO, J. C. (2018). Stable isotopes uncover trophic ecology of the West African crocodile (*Crocodylus suchus*). *Journal of Arid Environments* **148**, 6–13.
- *SCHALLER, G. B. & CRAWSHAW, P. G. (1980). Movement patterns of jaguar. *Biotropica* **12**, 161.
- SCHILLER, A., HUNSAKER, C. T., KANE, M. A., WOLFE, A. K., DALE, V. H., SUTER, G. W., RUSSELL, C. S., PION, G., JENSEN, M. H. & KONAR, V. C. (2001). Communicating ecological indicators to decision makers and the public. *Conservation Ecology* **5**, 19. Electronic file available at <http://www.consecol.org/vol5/iss1/art19> Accessed 03.03.2019
- SCHMITZ, O. J., HAWLENA, D. & TRUSSELL, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13**, 1199–1209.
- *SCHNEIDER, L., PELEJA, R. P., KLUCZKOVSKI, A., FREIRE, G. M., MARIONI, B., VOGT, R. C. & DA SILVA, R. (2012). Mercury concentration in the spectacled caiman and black caiman (Alligatoridae) of the Amazon: implications for human health. *Archives of Environmental Contamination and Toxicology* **63**, 270–279.
- SCHREIBER, S. & RUDOLF, V. H. (2008). Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. *Ecology Letters* **11**, 576–587.
- *SCOGNAMILLO, D. G. (2001). Ecological separation between jaguar and puma in a mosaic landscape in the Venezuelan Llanos. MSc Thesis, University of Florida, Gainesville, FL.
- SERGIO, F., NEWTON, I., MARCHESI, L. & PEDRINI, P. (2006). Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology* **43**, 1049–1055.
- SERGIO, F., SCHMITZ, O. J., KREBS, C. J., HOLT, R. D., HEITHAUS, M. R., WIRSING, A. J., RIPPLE, W. J., RITCHIE, E., AINLEY, D. & ORO, D. (2014). Towards a cohesive, holistic view of top predation: a definition, synthesis and perspective. *Oikos* **123**, 1234–1243.
- SHARMA, R. & SINGH, L. (2015). Status of mugger crocodile (*Crocodylus palustris*) in National Chambal Sanctuary after thirty years and its implications on conservation of Gharial (*Gavialis gangeticus*). *Zoo's Print* **30**, 9–16.
- SHEPARD, E. L., WILSON, R. P., REES, W. G., GRUNDY, E., LAMBERTUCCI, S. A. & VOSPER, S. B. (2013). Energy landscapes shape animal movement ecology. *The American Naturalist* **182**, 298–312.
- SHINE, R. (2011). How can we ensure that conservation policies are based on science, not emotion? *Pacific Conservation Biology* **17**, 6–10.
- SHINE, T., BOHME, W., NICKEL, H., THIES, D. F. & WILMS, T. (2001). Rediscovery of relict populations of the Nile crocodile *Crocodylus niloticus* in south-eastern Mauritania, with observations on their natural history. *Oryx* **35**, 260–262.
- *SHIRLEY, M. H., ODURO, W. & BEIBRO, H. Y. (2009). Conservation status of crocodiles in Ghana and cote-d'Ivoire, west Africa. *Oryx* **43**, 136–145.
- SHIRLEY, M. H., BURTNER, B., OSLISLY, R., SEBAG, D. & TESTA, O. (2017). Diet and body condition of cave-dwelling dwarf crocodiles (*Osteolaemus tetraspis*, Cope 1861) in Gabon. *African Journal of Ecology* **55**, 411–422.
- *SHOOP, C. R. & RUCKDESCHEL, C. A. (1990). Alligators as predators on terrestrial mammals. *American Midland Naturalist* **124**, 407.
- SILLIMAN, B. R., GROSHOLZ, E. & BERTNESS, M. D. (2009). *Human Impacts on Salt Marshes: A Global Perspective*. University of California Press, California.
- *SILLIMAN, B. R., HUGHES, B. B., GASKINS, L. C., HE, Q., TINKER, M. T., READ, A., NIFONG, J. & STEPP, R. (2018). Are the ghosts of nature's past haunting ecology today? *Current Biology* **28**, R532–R537.
- *DE SILVA, A. (2013). *The Crocodiles of Sri Lanka*. Published by the Author, Gampola.
- *DE SILVA, M. C., AMARASINGHE, A. T., DE SILVA, A. & KARUNARATHNA, D. S. (2011). Mugger crocodile (*Crocodylus palustris* Lesson, 1831) preys on a radiated tortoise in Sri Lanka. *Taprobanica: The Journal of Asian Biodiversity* **3**, 38.
- *SIMONCINI, M. S., PIÑA, C. I., CRUZ, F. B. & LARRIERA, A. (2011). Climatic effects on the reproductive biology of *Caiman latirostris* (Crocodylia: Alligatoridae). *Amphibia-Reptilia* **32**, 305–314.
- *SIMONCINI, M. S., CRUZ, F. B., LARRIERA, A. & PIÑA, C. I. (2014). Effects of climatic conditions on sex ratios in nests of broad-snouted caiman. *Journal of Zoology* **293**, 243–251.
- SINGH, H. & RAO, R. (2017). Status, threats and conservation challenges to key aquatic fauna (crocodile and dolphin) in National Chambal Sanctuary, India. *Aquatic Ecosystem Health & Management* **20**, 59–70.
- *SKAARE, J. U., INGBRIGTSEN, K., AULIE, A. & KANUI, T. I. (1991). Organochlorines in crocodile eggs from Kenya. *Bulletin of Environmental Contamination and Toxicology* **47**, 126–130.
- SLONE, D., RICE, K. & ALLEN, J. (2003). Model evaluates influence of Everglades restoration plan alternatives on alligator populations (Florida). *Ecological Restoration* **21**, 141–142.

- *SOMAWEERA, R., WEBB, J. K. & SHINE, R. (2011). It's a dog-eat-croc world: dingo predation on the nests of freshwater crocodiles in tropical Australia. *Ecological Research* **26**, 957–967.
- SOMAWEERA, R., SHINE, R., WEBB, J., DEMPSTER, T. & LETNIC, M. (2012). Why does vulnerability to toxic invasive cane toads vary among populations of Australian freshwater crocodiles? *Animal Conservation* **16**, 86–96.
- SOMAWEERA, R., BRIEN, M. & SHINE, R. (2013). The role of predation in shaping crocodylian natural history. *Herpetological Monographs* **27**, 23–51.
- SOMAWEERA, R., WOODS, D. & SONNEMAN, T. (2014). A note on the Australian freshwater crocodiles inhabiting Tunnel Creek cave, West Kimberley. *Records of the Western Australian Museum* **82**, 29.
- SOMAWEERA, R., BRIEN, M. L., PLATT, S. G., MANOLIS, C. & WEBBER, B. L. (2018a). Direct and indirect interactions with vegetation shape crocodylian ecology at multiple scales. *Freshwater Biology* **64**, 257–268.
- SOMAWEERA, R., RHIND, D., REYNOLDS, S., EISEMBERG, C., SONNEMAN, T. & WOODS, D. (2018b). Observations of mammalian feeding by Australian freshwater crocodiles (*Crocodylus johnstoni*) in the Kimberley region of Western Australia. *Records of the Western Australian Museum* **33**, 103–107.
- SOMAWEERA, R., BRIEN, M. L., SONNEMAN, T., DIDHAM, R. K. & WEBBER, B. L. (2019). Absence of evidence is not evidence of absence: knowledge shortfalls threaten the effective conservation of freshwater crocodiles. *Global Ecology and Conservation* **20**, e00773.
- SOULÉ, M. E., ESTES, J. A., MILLER, B. & HONNOLD, D. L. (2005). Strongly interacting species: conservation policy, management, and ethics. *Bioscience* **55**, 168–176.
- *STANIEWICZ, A., BEHLER, N., DHARMASYAH, S. & JONES, G. (2018). Niche partitioning between juvenile sympatric crocodylians in Mesangat, East Kalimantan, Indonesia. *Raffles Bulletin of Zoology* **66**, 528–537.
- *STATON, M. & DIXON, J. (1977). Breeding biology of the spectacled caiman, *Caiman crocodilus crocodilus*, in the Venezuelan Llanos: Wildlife Research Report 5. Washington, D.C.
- STATON, M. A., EDWARDS, H. M. JR., BRISBIN, I. L. JR., JOANEN, T. & MCNEASE, L. (1990). Protein and energy relationships in the diet of the American alligator (*Alligator mississippiensis*). *The Journal of Nutrition* **120**, 775–785.
- STEVENSON, C. (2015). Conservation of the Indian gharial *Gavialis gangeticus*: successes and failures. *International Zoo Yearbook* **49**, 150–161.
- STIER, A. C., SAMHOURI, J. F., NOVAK, M., MARSHALL, K. N., WARD, E. J., HOLT, R. D. & LEVIN, P. S. (2016). Ecosystem context and historical contingency in apex predator recoveries. *Science Advances* **2**, e1501769.
- *STRONG, D. R. & FRANK, K. T. (2010). Human involvement in food webs. *Annual Review of Environment and Resources* **35**, 1–23.
- SUBALUSKY, A. L., FITZGERALD, L. A. & SMITH, L. L. (2009). Ontogenetic niche shifts in the American alligator establish functional connectivity between aquatic systems. *Biological Conservation* **142**, 1507–1514.
- SUBALUSKY, A. L., DUTTON, C. L., ROSI, E. J. & POST, D. M. (2017). Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences of the United States of America* **114**, 7647–7652.
- *SUTHERLAND, R. W. & SUTHERLAND, E. G. (2003). Status of the flatback sea turtle (*Natator depressus*) rookery on Crab Island, Australia, with notes on predation by crocodiles. *Chelonian Conservation and Biology* **4**, 612–619.
- SWANEPOEL, D. (1999). *Movements, nesting and the effects of pollution on the Nile crocodile (Crocodylus niloticus) in the Olifants River*. University of KwaZulu-Natal, Kruger National Park.
- *SWANEPOEL, D. G. J., FERGUSON, N. S. & PERRIN, M. R. (2000). Nesting ecology of Nile crocodiles (*Crocodylus niloticus*) in the Olifants River, Kruger National Park. *Koedoe* **43**, 35–46.
- TAYLOR, J. A. (1979). The foods and feeding habits of subadult *Crocodylus porosus* Schneider in Northern Australia. *Wildlife Research* **6**, 347–359.
- *TELLEZ, M. & MERCHANT, M. (2015). Biomonitoring heavy metal pollution using an aquatic apex predator, the American Alligator, and its parasites. *PLoS One* **10**, e0142522.
- TELLEZ, M. & NIFONG, J. (2014). Gastric nematode diversity between estuarine and inland freshwater populations of the American alligator (*Alligator mississippiensis*, Daudin 1802), and the prediction of intermediate hosts. *International Journal for Parasitology: Parasites and Wildlife* **3**, 227–235.
- TELLEZ, M. & SUNG, H. (2018). Unveiling the host-parasite dynamic of alligators and their endoparasites. In *American Alligators: Habitats, Behavior, and Threats* (eds S. C. HENKE and C. EVERSOLE). Nova Science Publishers, New York City, New York.
- *THORBJARNARSON, J. B. (1988). The status and ecology of the American crocodile in Haiti. *Bulletin of the Florida State Museum, Biological Sciences* **33**, 1–86.
- THORBJARNARSON, J. B. (1993). Diet of the spectacled caiman (*Caiman crocodilus*) in the central Venezuelan llanos. *Herpetologica* **49**, 108–117.
- *THORBJARNARSON, J. B. (1996). Reproductive characteristics of the order Crocodylia. *Herpetologica* **52**, 8–24.
- *THORBJARNARSON, J. B. (1999). Crocodile tears and skins: international trade, economic constraints, and limits to the sustainable use of crocodylians. *Conservation Biology* **13**, 465–470.
- THORBJARNARSON, J. B. (2010). American crocodile *Crocodylus acutus*. crocodylians. *Status Survey and Conservation Action Plan* **3**, 46–53.
- *THORBJARNARSON, J. B. & HERNÁNDEZ, G. (1993). Reproductive ecology of the Orinoco crocodile (*Crocodylus intermedius*) in Venezuela. II. Reproductive and Social Behavior. *Journal of Herpetology* **27**, 363–370.
- THORBJARNARSON, J. & WANG, X. (2010). *The Chinese Alligator: Ecology, Behavior, Conservation, and Culture*. John Hopkins University Press, Baltimore, MD.
- *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.
- *THORBJARNARSON, J., WANG, X., MING, S., HE, L., DING, Y., WU, Y. & MCMURRY, S. T. (2002). Wild populations of the Chinese alligator approach extinction. *Biological Conservation* **103**, 93–102.
- *THORBJARNARSON, J., MAZZOTTI, F., SANDERSON, E., BUTRAGO, F., LAZCANO, M., MINKOWSKI, K., MUÑOZ, M., PONCE, P., SIGLER, L., SOBERON, R., TRELANCIA, A. M. & VELASCO, A. (2006). Regional habitat conservation priorities for the American crocodile. *Biological Conservation* **128**, 25–36.
- *TIKADER, B.K.D. (1983). *Threatened animals of India*. In *Threatened animals of India*. Zoological Survey of India, Calcutta.
- *TINLEY, K. L. (1976). *The ecology of Tongaland*. Natal Branch of the Wildlife Society of South Africa. Durban, South Africa.
- *TOONEN, H. (2003). The sacred crocodiles of Bazoule. *Crocodyle Specialist Group Newsletter* **22**.
- *TORRALVO, K., BOTERO-ARIAS, R. & MAGNUSON, W. E. (2017a). Temporal variation in black caiman nest predation in Varzea of central Brazilian Amazonia. *PLoS One* **12**, e0183476.
- *TORRALVO, K., RABELO, R. M., ANDRADE, A. & BOTERO-ARIAS, R. (2017b). Tool use by Amazonian capuchin monkeys during predation on caiman nests in a high-productivity forest. *Primates* **58**, 279–283.
- *TREMBLAY, P. (2003). Crocodiles and top end visitors: a meta-review of tourist perceptions, motivations and attitudes towards a controversial local icon. Riding the Wave of Tourism and Hospitality Research: Proceedings of the CAUTHE Conference, Southern Cross University Press.
- TREVES, A. & KARANTH, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* **17**, 1491–1499.
- TREVES, A., NAUGHTON-TREVES, L., HARPER, E. K., MLADENOFF, D. J., ROSE, R. A., SICKLEY, T. A. & WYDEVEN, A. P. (2004). Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology* **18**, 114–125.
- *TRILLANES, C. E., PÉREZ-JIMÉNEZ, J. C., ROSÍLES-MARTÍNEZ, R. & GONZÁLEZ-JAUREGUI, M. (2014). Metals in the caudal scutes of Morelet's crocodile (*Crocodylus moreletii*) from the southern Gulf of Mexico. *Bulletin of Environmental Contamination and Toxicology* **93**, 423–428.
- *TUBERVILLE, T. D., SCOTT, D. E., METTS, B. S., FINGER, J. W. & HAMILTON, M. T. (2016). Hepatic and renal trace element concentrations in American alligators (*Alligator mississippiensis*) following chronic dietary exposure to coal fly ash contaminated prey. *Environmental Pollution* **214**, 680–689.
- *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.
- *TUCKER, A. D., LIMPUS, C. J., MCCALLUM, H. I. & MCDONALD, K. R. (1997a). Movements and home ranges of *Crocodylus johnstoni* in the Lynd River, Queensland. *Wildlife Research* **24**, 379–396.
- *TUCKER, A. D., MCCALLUM, H. I. & LIMPUS, C. J. (1997b). Habitat use by *Crocodylus johnstoni* in the Lynd River, Queensland. *Journal of Herpetology* **31**, 114–121.
- *VELASCO, A., COLOMINE, G., VILLARROEL, G., CAMACARO, O., DE SOLA, R., LEÓN, N., OROPEZA, E., PÉREZ-HERNÁNDEZ, R., PINO, T., QUERO, M., RAMOS, J., RAMOS, S., SÁNCHEZ, G. & VÁZQUEZ, W. (1996). Surveying nest of spectacled caiman (*Caiman crocodilus*) in ecological areas of Venezuelan llanos. In *Crocodyles. Proceedings of the 13th Working Meeting of the IUCN-SSC Crocodile Specialist Group* p. IUCN-SSC Crocodile Specialist Group, Gland, Switzerland.
- VELO-ANTÓN, G., GODINHO, R., CAMPOS, J. C. & BRITO, J. C. (2014). Should I stay or should I go? Dispersal and population structure in small, isolated desert populations of West African crocodiles. *PLoS One* **9**, e94626.
- *VENEGAS-ANAYA, M., ESCOBEDO-GALVÁN, A. H., BALAGUERA-REINA, S. A., LOWRANCE, F., SANJUR, O. I. & DENSMORE, L. D. III (2015). Population Ecology of American Crocodile (*Crocodylus acutus*) in Coiba National Park, Panama. *Journal of Herpetology* **49**, 349–357.
- *VIEIRA, L. M., NUNES, V. D. S., AMARAL, M. C. D. A., OLIVEIRA, A. C., HAUSER-DAVIS, R. A. & CAMPOS, R. C. (2011). Mercury and methyl mercury ratios in caimans (*Caiman crocodilus yacare*) from the Pantanal area, Brazil. *Journal of Environmental Monitoring* **13**, 280–287.

- *VILLAMARÍN, F., MARIANI, B., THORBJARNARSON, J. B., NELSON, B. W., BOTERO-ARIAS, R. & MAGNUSON, W. E. (2011). Conservation and management implications of nest-site selection of the sympatric crocodylians *Melanosuchus niger* and *Caiman crocodylus* in Central Amazonia, Brazil. *Biological Conservation* **144**, 913–919.
- VILLAMARÍN, F., JARDINE, T. D., BUNN, S. E., MARIANI, B. & MAGNUSON, W. E. (2017). Opportunistic top predators partition food resources in a tropical freshwater ecosystem. *Freshwater Biology* **62**, 1389–1400.
- VILLAMARÍN, F., JARDINE, T. D., BUNN, S. E., MARIANI, B. & MAGNUSON, W. E. (2018). Body size is more important than diet in determining stable-isotope estimates of trophic position in crocodylians. *Scientific Reports* **8**, 1–11.
- VILLANUEVA, M. C., OUEDRAOGO, M. & MOREAU, J. (2006). Trophic relationships in the recently impounded Bagré reservoir in Burkina Faso. *Ecological Modelling* **191**, 243–259.
- *VILLEGAS, A. & SCHMITTER-SOTO, J. J. (2008). Feeding habits of the American crocodile, *Crocodylus acutus* (Cuvier, 1807) (Reptilia: Crocodylidae) in the southern coast of Quintana Roo, Mexico. *Acta Zoológica Mexicana* **24**, 117–124.
- *VITT, L. J. & CALDWELL, J. P. (2014). *Herpetology: An Introductory Biology of Biology of Amphibians and Reptiles*, 4th Edition. Academic Press, Cambridge, UK.
- VLIET, K. (2001). Reproductive biology of crocodylians. In *Crocodylian Biology and Captive Management* (eds K. A. VLIET and J. D. GROVES), pp. 1–35. AZA Professional Development Program, Silver Springs, MD.
- *VYAS, R. (2012). Current status of marsh crocodiles *Crocodylus palustris* (Reptilia: Crocodylidae) in Vishwamitri River, Vadodara City, Gujarat, India. *Journal of Threatened Taxa* **4**, 3333–3341.
- WADDLE, J. H., BRANDT, L. A., JEFFERY, B. M. & MAZZOTTI, F. J. (2015). Dry years decrease abundance of American alligators in the Florida Everglades. *Wetlands* **35**, 865–875.
- *WAITKUIWAIT, W. E. (1985). Investigations of the breeding biology of the west-african slender-snouted crocodile *Crocodylus cataphractus* Cuvier, 1824. *Amphibia-Reptilia* **6**, 387–399.
- WAITKUIWAIT, W. E. (1986). Contribution à l'étude des crocodiles en Afrique de l'ouest. *Nature et Faune, Abidjan* **1**, 13–29.
- WAKE, D. B. & VREDENBURG, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences* **105**, 11466–11473.
- 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.
- WALLACH, A. D., JOHNSON, C. N., RITCHIE, E. G. & O'NEILL, A. J. (2010). Predator control promotes invasive dominated ecological states. *Ecology Letters* **13**, 1008–1018.
- WALLACH, A. D., IZHAKI, I., TOMS, J. D., RIPPLE, W. J. & SHANAS, U. (2015). What is an apex predator? *Oikos* **124**, 1453–1461.
- WALTERS, C. J. (1986). *Adaptive Management of Renewable Resources*. Macmillan Publishers Ltd, New York, NY.
- *WARNER, J.K. (2015). *Morphometrics, ecotoxicology and stable isotope ecology of Nile crocodiles (Crocodylus niloticus) in KwaZulu-Natal, South Africa*. PhD Thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa.
- WATTS, K. & HANDLEY, P. (2010). Developing a functional connectivity indicator to detect change in fragmented landscapes. *Ecological Indicators* **10**, 552–557.
- WCSP (1997). *Philippine Red Data Book*. Wildlife Conservation Society of the Philippines, Quezon City.
- WEBB, G. (2014). *Wildlife Conservation: In the Belly of the Beast*. Charles Darwin University Press, Darwin.
- *WEBB, G. J. W. & MANOLIS, C. S. (1989). *Crocodyles of Australia*. Reed Books Pty, Ltd., Frenchs Forest, Australia.
- *WEBB, G. J. W. & MESSEL, H. (1978). Movement and dispersal patterns of *Crocodylus porosus* in some rivers of Arnhem Land, Northern Australia. *Wildlife Research* **5**, 263–283.
- *WEBB, G. J. W., MESSEL, H. & MAGNUSON, W. (1977). The nesting of *Crocodylus porosus* in Arnhem Land, Northern Australia. *Copeia* **1977**, 238–249.
- 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.
- WEBB, G. J. W., MANOLIS, S. & BUCKWORTH, R. (1983). *Crocodylus johnstoni* in the McKinlay River area N. T. II. Dry-season habitat selection and an estimate of the total population size. *Australian Wildlife Research* **10**, 373–382.
- WEBB, G. J. W., HOLLIS, G. J. & MANOLIS, S. C. (1991). Feeding, growth, and food conversion rates of wild juvenile saltwater crocodiles (*Crocodylus porosus*). *Journal of Herpetology* **25**, 462–473.
- *WESSELS, C. L., BLAKE, D. K., TANNOCK, J. & PHELPS, R. J. (1980). Chlorinated hydrocarbon insecticide residues in *Crocodylus niloticus* eggs from Lake Kariba, Zimbabwe. *Transactions of the Zimbabwe Scientific Association* **60**, 11–17.
- *WHEATLEY, P.V. (2010). *Understanding saltwater tolerance and marine resource use in the Crocodylia: A stable isotope approach*. PhD Thesis, University of California, Santa Cruz, CA.
- *WHEATLEY, P. V., PECKHAM, H., NEWSOME, S. D. & KOCH, P. L. (2012). Estimating marine resource use by the American crocodile *Crocodylus acutus* in southern Florida, USA. *Marine Ecology Progress Series* **447**, 211–229.
- *WHITAKER, R. (1977). Note on the status of Gir crocodiles. *Journal of the Bombay Natural History Society* **75**, 224–227.
- *WHITAKER, R. & WHITAKER, Z. (1979). Preliminary crocodile survey – Sri Lanka. *Journal of the Bombay Natural History Society* **76**, 66–85.
- *WHITAKER, R. & WHITAKER, Z. (1984). Reproductive biology of Mugger. *Journal of the Bombay Natural History Society* **81**, 119–127.
- WHITAKER, R. & WHITAKER, Z. (1989). Ecology of the mugger crocodile. In *Crocodyles. Their Ecology, Management and Conservation*, pp. 276–297. Crocodile Specialist Group IUCN, Gland, Switzerland.
- *WHITAKER, R., BARR, B., DE SILVA, A. & RATNASIRI, P. (2007). Observations on burrows dug by mugger crocodiles (*Crocodylus palustris*) in Bundala National Park, Sri Lanka. *Journal of the Bombay Natural History Society* **104**, 19–24.
- WHITFIELD, A. K. & BLABER, S. J. (1979). Predation on striped mullet (*Mugil cephalus*) by *Crocodylus niloticus* at St. Lucia, South Africa. *Copeia* **1979**, 266–269.
- *WHITING, S. D. & WHITING, A. U. (2011). Predation by the saltwater crocodile (*Crocodylus porosus*) on sea turtle adults, eggs, and hatchlings. *Chelonian Conservation and Biology* **10**, 198–205.
- *WINGARD, G. L. & LORENZ, J. J. (2014). Integrated conceptual ecological model and habitat indices for the southwest Florida coastal wetlands. *Ecological Indicators* **44**, 92–107.
- WOODWARD, A., HINES, T., ABERCROMBIE, C. & HOPE, C. (1984). Spacing patterns in alligator nests. *Journal of Herpetology* **18**, 8–12.
- WOODWARD, G., PERKINS, D. M. & BROWN, L. E. (2010). Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2093–2106.
- *WU, T. H., RAINWATER, T. R., PLATT, S. G., MCMURRY, S. T. & ANDERSON, T. A. (2000a). DDE in eggs of two crocodile species from Belize. *Journal of Agricultural and Food Chemistry* **48**, 6416–6420.
- WU, T. H., RAINWATER, T. R., PLATT, S. G., MCMURRY, S. T. & ANDERSON, T. A. (2000b). Organochlorine contaminants in morelet's crocodile (*Crocodylus moreletii*) eggs from Belize. *Chemosphere* **40**, 671–678.
- *WU, T. H., CANAS, J. E., RAINWATER, T. R., PLATT, S. G., MCMURRY, S. T. & ANDERSON, T. A. (2006). Organochlorine contaminants in complete clutches of Morelet's crocodile (*Crocodylus moreletii*) eggs from Belize. *Environmental Pollution* **144**, 151–157.
- *WU, T., HONG, B., WU, X., WU, J., WANG, X., YI, Z., ZHAO, J., ZHAN, M. & MAI, B. (2014). Persistent halogenated compounds in captive Chinese alligators (*Alligator sinensis*) from China. *Chemosphere* **110**, 23–30.
- *XU, Q., FANG, S., WANG, Z. & WANG, Z. (2006). Heavy metal distribution in tissues and eggs of Chinese alligator (*Alligator sinensis*). *Archives of Environmental Contamination and Toxicology* **50**, 580–586.
- *ZAFAR, M. & MALIK, M. F. (2018). A review on status and conservation of mugger crocodile. *Journal of Advanced Botany and Zoology* **6**, 1–4.
- *ZHANG, F., XIAO-BING, W., WEI-ZHI, M. & JIA-LONG, Z. (2006). Ecology on the making nest and laying eggs of chinese alligator (*Alligator sinensis*) under artificial feeding conditions. *Zoological Research* **2**, 151–156.

XIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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 and Ecological indicators.

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.

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.

Family*	Taxa	IUCN Red List Category**	Claims (untested)				Demonstration (experiment or observations)			
			Apex predators/Keystone species	Ecosystem engineers	Cross-ecosystem linkages	Ecological indicators	Apex predators/Keystone species	Ecosystem engineers	Cross-ecosystem linkages	Ecological indicators
Americas										
A	<i>Alligator mississippiensis</i> (American alligator)	LC	Kellogg (1929); Harper (1930); McIlhenny (1935); Shoop & Ruckdeschel (1990); Gunderson (1994); Bondavalli & Ulanowicz (1999); Keddy <i>et al.</i> (2007, 2009); Strong & Frank (2010); Rosenblatt <i>et al.</i> (2013a); Atwood <i>et al.</i> (2015); Hinman (2015); Nifong & Lowers (2017); Gilliland <i>et al.</i> (2018)	Harper (1930); McIlhenny (1935); Loveless (1959); Carr (1973); Jones <i>et al.</i> (1994); Gunderson (1994); Pintor & Soluk (2006)	McIlhenny (1935)	Davis <i>et al.</i> (2005); Ogden (2005); Doren <i>et al.</i> (2009)	Martin & Hight, (1977); Nifong & Silliman (2013); Nell & Frederick (2015); Nell <i>et al.</i> (2016)	Craighead (1968); Campbell (1972); Kushlan (1974); Deitz & Jackson (1979); Deitz & Hines (1980); Kushlan & Kushlan (1980); Hunt & Ogden (1991); Hall & Meier (1993); Mazzotti & Brandt (1994); Campbell & Mazzotti (2004); Palmer & Mazzotti (2004); Brazaitis & Watanabe (2011); Merchant <i>et al.</i> (2014)	Campbell (1972); Fleming <i>et al.</i> (1976); Delany & Abercrombie (1986); Palis (1989); Shoop & Ruckdeschel (1990); Subalusky <i>et al.</i> (2009); Wheatley (2010); Brazaitis & Watanabe (2011); Lance <i>et al.</i> (2011); Nifong & Frick (2011); Nifong <i>et al.</i> (2011, 2015); Rosenblatt & Heithaus (2011); Saalfeld <i>et al.</i> (2011); Rosenblatt <i>et al.</i> (2013a,b, 2015); Elsey <i>et al.</i> (2014); Fujisaki <i>et al.</i> (2014); Nell & Frederick (2015); Nifong (2016); Nifong & Silliman (2017); Gilliland <i>et al.</i> (2018); Silliman <i>et al.</i> (2018)	Mazzotti & Brandt (1994); Guillette <i>et al.</i> (2000); Khan & Tansel (2000); Guillette & Gunderson (2001); Guillette & Edwards (2008); Fujisaki <i>et al.</i> (2009, 2012); Mazzotti <i>et al.</i> (2009); J.W. Campbell <i>et al.</i> (2010); Jeffery & Cherkiss (2012); Horai <i>et al.</i> (2014); Tellez & Merchant (2015); Boggs <i>et al.</i> (2016); Brandt <i>et al.</i> (2016); Gunderson <i>et al.</i> (2016); Tuberville <i>et al.</i> (2016); Bangma <i>et al.</i> (2017); Nilsen <i>et al.</i> (2017); Silliman <i>et al.</i> (2018)

A	<i>Caiman crocodilus</i> (spectacled caiman)	LC	Fittkau (1970, 1973); Brazaitis <i>et al.</i> (1998); Balaguera-Reina & González-Maya (2010)	Brazaitis <i>et al.</i> (1998)				Campbell (1972); Staton & Dixon (1977); Magnusson <i>et al.</i> (1987); Ouboter & Nanhoe (1987, 1988); Thorbjarnarson (1993); Allsteadt (1994); Velasco <i>et al.</i> (1996); Brazaitis & Watanabe (2011); Villamarín <i>et al.</i> (2011)	Campbell (1972); Staton & Dixon (1977); Magnusson <i>et al.</i> (1987); Ouboter & Nanhoe (1987, 1988); Thorbjarnarson (1993); Allsteadt (1994); Velasco <i>et al.</i> (1996); Da Silveira & Magnusson (1999); Scognamillo (2001); Da Silveira <i>et al.</i> (2010); Brazaitis & Watanabe (2011); Villamarín <i>et al.</i> (2011); Barão-Nóbrega <i>et al.</i> (2014); Campos <i>et al.</i> (2015); Torralvo <i>et al.</i> (2017b)	Brazaitis <i>et al.</i> (1996); Escobedo-Galván <i>et al.</i> (2012); Schneider <i>et al.</i> (2012); Eggins <i>et al.</i> (2015)
A	<i>Caiman latirostris</i> (broad-snouted caiman)	LC	Brazaitis <i>et al.</i> (1998)	Brazaitis <i>et al.</i> (1998)	Vitt & Caldwell (2014)	Rey <i>et al.</i> (2006); Poletta <i>et al.</i> (2008)		Larriera & Piña (2000); Montini <i>et al.</i> (2006); Brazaitis & Watanabe (2011); Marcó <i>et al.</i> (2015)	Grigg <i>et al.</i> (1998); Larriera & Piña (2000); Montini <i>et al.</i> (2006); Brazaitis & Watanabe (2011); Marcó <i>et al.</i> (2015)	Poletta <i>et al.</i> (2008, 2009); Simoncini <i>et al.</i> (2011, 2014); Latorre <i>et al.</i> (2016)
A	<i>Caiman yacare</i> (Jacaré caiman)	LC	Santos <i>et al.</i> (1996); Brazaitis <i>et al.</i> (1998)	Brazaitis <i>et al.</i> (1998)	Vitt & Caldwell (2014)			Cintra (1988); Campos (1993); Brazaitis & Watanabe (2011)	Schaller & Crawshaw (1980); Cintra (1988); Campos (1993); Santos <i>et al.</i> (1996); Campos <i>et al.</i> (2003, 2006); de Acevedo & Murray (2007); Brazaitis & Watanabe (2011); Campos & Mourão (2015)	Campos & Magnusson (1995); Brazaitis <i>et al.</i> (1996); Campbell <i>et al.</i> (2008); Vieira <i>et al.</i> (2011); Rivera <i>et al.</i> (2016)
A	<i>Melanosuchus niger</i> (black caiman)	LC	Fittkau (1970, 1973); Brazaitis <i>et al.</i> (1998); de Miranda (2017)	Brazaitis <i>et al.</i> (1998)	Vitt & Caldwell (2014)			Campbell (1972); Brazaitis & Watanabe (2011); Villamarín <i>et al.</i> (2011); Maffei & Da Silveira (2013); Torralvo <i>et al.</i> (2017a)	Campbell (1972); Magnusson <i>et al.</i> (1987); Da Silveira & Magnusson (1999); Da Silveira <i>et al.</i> (2010); Brazaitis & Watanabe (2011); Villamarín <i>et al.</i> (2011); Torralvo <i>et al.</i> (2017a,b)	Schneider <i>et al.</i> (2012); Correia <i>et al.</i> (2014); Eggins <i>et al.</i> (2015)

A	<i>Paleosuchus palpebrosus</i> (Cuvier's dwarf caiman)	LC	Fittkau (1970)					Campbell (1972); Brazaitis & Watanabe (2011); Campos & Mourão (2015)	Campbell (1972); Magnusson <i>et al.</i> (1987); Brazaitis & Watanabe (2011); Campos & Mourão (2015)	
A	<i>Paleosuchus trigonatus</i> (Schneider's dwarf caiman)	LC	Fittkau (1970)					Magnusson <i>et al.</i> (1990); Brazaitis & Watanabe (2011); Campos <i>et al.</i> (2016)	Magnusson <i>et al.</i> (1987); Brazaitis & Watanabe (2011); Sampaio <i>et al.</i> (2013); Campos <i>et al.</i> (2016)	
C	<i>Crocodylus acutus</i> (American crocodile)	VU	Ogden <i>et al.</i> (2005); Heithaus <i>et al.</i> (2008 <i>b</i>); Balaguera- Reina & González- Maya (2010)		Heithaus <i>et al.</i> (2008 <i>b</i>)	Davis <i>et al.</i> (2005); Richards <i>et al.</i> (2004); Ogden <i>et al.</i> (2005); Thorbjarnarson <i>et al.</i> (2006); Doren <i>et al.</i> (2009); Wingard & Lorenz (2014)	Ortiz <i>et al.</i> (1997)	Campbell (1972); Medem (1981); Thorbjarnarson (1988); Kushlan & Mazzotti (1989); Brazaitis & Watanabe (2011)	Campbell (1972); Medem (1981); Thorbjarnarson (1988); Kushlan & Mazzotti (1989); Mazzotti (1989); Ortiz <i>et al.</i> (1997); Mazzotti & Brandt (1994); Platt & Thorbjarnarson (2000); Casas- Andreu & Quiroz (2003); Villegas & Schmitter-Soto (2008); Wheatley (2010); Brazaitis & Watanabe (2011); Wheatley <i>et al.</i> (2012); Platt <i>et al.</i> (2013); Venegas- Anaya <i>et al.</i> (2015); Balaguera- Reina <i>et al.</i> (2016, 2018)	Wu <i>et al.</i> (2000 <i>a</i>); Mazzotti <i>et al.</i> (2007, 2009); Rainwater <i>et al.</i> (2007); Charruau <i>et al.</i> (2010)
C	<i>Crocodylus intermedius</i> (Orinoco crocodile)	CR	de Miranda (2017)						Campbell (1972); Medem (1981); Thorbjarnarson & Hernández (1993); Brazaitis & Watanabe (2011)	
C	<i>Crocodylus moreletii</i> (Morelet's crocodile)	LC						Campbell (1972); Platt <i>et al.</i> (2008); Brazaitis & Watanabe (2011); Escobedo-Galván <i>et al.</i> (2011)	Campbell (1972); Pérez-Higareda <i>et al.</i> (1989); Platt <i>et al.</i> (2006 <i>a</i> , 2007, 2008); Brazaitis & Watanabe (2011)	Wu <i>et al.</i> (2000 <i>a,b</i> , 2006); Rainwater <i>et al.</i> (2002, 2007); Pepper <i>et al.</i> (2004); Gonzalez- Jauregui <i>et al.</i> (2012); Mazzotti <i>et al.</i> (2012); Trillanes <i>et al.</i> (2014); Buenfil- Rojas <i>et al.</i> (2015, 2018)

C	<i>Crocodylus rhombifer</i> (Cuban crocodile)	CR	de Miranda (2017)					Campbell (1972); Thorbjarnarson (1996); Brazaitis & Watanabe (2011)	Campbell (1972); Brazaitis & Watanabe (2011)	
Africa										
C	<i>Crocodylus niloticus</i> (Nile crocodile)	LC	Cott (1961); Pooley (1973); Tinley (1976); Bourquin (2007); Ashton (2010); Adugna <i>et al.</i> (2017); de Miranda (2017)	de Miranda (2017)	Vitt & Caldwell (2014)	Pooley (1973); Tinley (1976); Swanepoel <i>et al.</i> (2000); Joubert & van Gogh (2007); Ashton (2010); Adugna <i>et al.</i> (2017)	Chihona (2014); Subalusky <i>et al.</i> (2017)		Modha (1967, 1968); Pooley (1969); Campbell (1972); Hutton (1989); Kofron (1989, 1993); Games (1990); Swanpoel <i>et al.</i> (2000); Wallace & Leslie (2008); Brazaitis & Watanabe (2011); Radloff <i>et al.</i> (2012); Calverly & Downs (2015, 2017); Chihona (2014); Warner (2015); Combrink <i>et al.</i> (2017); Subalusky <i>et al.</i> (2017)	Wessels <i>et al.</i> (1980); Phelps <i>et al.</i> (1986, 1989); Skaare <i>et al.</i> (1991); Bishop <i>et al.</i> (2009); Botha <i>et al.</i> (2011); Ferreira & Pienaar (2011); Dabrowski <i>et al.</i> (2013); Warner (2015); Buah-Kwofie <i>et al.</i> (2018); du Preez <i>et al.</i> (2018)
C	<i>Crocodylus suchus</i> (West African crocodile)	NA***	Shirley <i>et al.</i> (2009)			Shirley <i>et al.</i> (2009)				
C	<i>Mecistops cataphractus</i> (West African slender-snouted crocodile)	CR	Shirley <i>et al.</i> (2009)			Shirley <i>et al.</i> (2009)		Campbell (1972); Waitkuwait (1985); Brazaitis & Watanabe (2011)	Campbell (1972); Waitkuwait (1985); Brazaitis & Watanabe (2011)	
C	<i>M. leptorhynchus</i> (Central African slender-snouted crocodile)	NA***								
C	<i>Osteolaemus osborni</i> (Congo dwarf crocodile)	NA***								
C	<i>O. tetraspis</i> (African dwarf crocodile)	VU	Shirley <i>et al.</i> (2009)	de Miranda (2017)		Shirley <i>et al.</i> (2009)		Campbell (1972); Brazaitis & Watanabe (2011)	Campbell (1972); Brazaitis & Watanabe (2011)	
Asia & Austral-Papua										
A	<i>Alligator sinensis</i> (Chinese alligator)	CR			Vitt & Caldwell (2014)			Cheng-Kuan (1957); Campbell (1972); Thorbjarnarson <i>et al.</i> (2001); Zhang <i>et al.</i> (2006); Thorbjarnarson & Wang (2010); Brazaitis & Watanabe (2011)	Campbell (1972); Brazaitis & Watanabe (2011)	Ding <i>et al.</i> (2001); Thorbjarnarson <i>et al.</i> (2002); Xu <i>et al.</i> (2006); Wu <i>et al.</i> (2014)

C	<i>Crocodylus johnstoni</i> (Australian freshwater crocodile)	LC			Vitt & Caldwell (2014)			Campbell (1972); Webb & Manolis (1989); Tucker <i>et al.</i> (1996, 1997b); Brazaitis & Watanabe (2011); Somaweera, Webb, & Shine (2011)	Campbell (1972); Webb & Manolis (1989); Tucker <i>et al.</i> (1997b)	Jeffree <i>et al.</i> (2005); Letnic <i>et al.</i> (2008)
C	<i>Crocodylus mindorensis</i> (Phillippine crocodile)	CR	Banks (2005); Manalo & Alcala (2015)	WCSP (1997)		Manalo & Alcala (2015)		Brazaitis & Watanabe (2011)	Brazaitis & Watanabe (2011)	Bucol <i>et al.</i> (2014)
C	<i>Crocodylus novaeguineae</i> (New Guinea crocodile)	LC						Campbell (1972); Hall & Johnson (1987); Brazaitis & Watanabe (2011)	Campbell (1972); Hall & Johnson (1987); Brazaitis & Watanabe (2011)	
C	<i>Crocodylus palustris</i> (mugger crocodile)	VU	McNeely & Sochaczewski (1991); Bhatnagar & Mahur (2010); Chang <i>et al.</i> (2012); de Miranda (2017); Zafar & Malik (2018)	Zafar & Malik (2018)	Vitt & Caldwell (2014); Zafar & Malik (2018)			Tikader (1983); Whitaker & Whitaker (1984, 1989); Poe (1996); Mobaraki (2002); Whitaker <i>et al.</i> (2007); Brazaitis & Watanabe (2011); Chang <i>et al.</i> (2012); Vyas (2012)	Ghalib <i>et al.</i> (1981); Whitaker (1977); Whitaker & Whitaker (1979, 1989); Mobaraki & Abtin (2007); Whitaker <i>et al.</i> (2007); Bhatnagar & Mahur (2010); Brazaitis & Watanabe (2011); Corlett (2011); De Silva <i>et al.</i> (2011); Vyas (2012)	Chang <i>et al.</i> (2012, 2014)
C	<i>Crocodylus porosus</i> (estuarine crocodile)	LC	Heithaus <i>et al.</i> (2008b); Doody (2009); Fijn (2013); de Miranda (2017)	de Miranda (2017)	Heithaus <i>et al.</i> (2008b); Vitt & Caldwell (2014)		Sutherland & Sutherland (2003); Whiting & Whiting (2011)	Campbell (1972); Webb <i>et al.</i> (1977); Magnusson (1980); Webb & Manolis (1989); Sutherland & Sutherland (2003); Taylor (1979); Magnusson (1980); Webb & Manolis (1989); Brazaitis & Watanabe (2011); Fukuda & Cuff (2013)	Campbell (1972); Webb <i>et al.</i> (1977); Webb & Messel (1978); Taylor (1979); Magnusson (1980); Webb & Manolis (1989); Sutherland & Sutherland (2003); Kay (2004); Read <i>et al.</i> (2007); Brien <i>et al.</i> (2008); H.A. Campbell <i>et al.</i> (2010); Brazaitis & Watanabe (2011); Whiting & Whiting (2011); Fukuda & Cuff (2013); Hanson <i>et al.</i> (2015); Adame <i>et al.</i> (2018)	Markich <i>et al.</i> (2002)

C	<i>Crocodylus siamensis</i> (Siamese crocodile)	CR	Staniewicz <i>et al.</i> (2018)					Campbell (1972); Platt <i>et al.</i> (2006b, 2012); Brazaitis & Watanabe (2011); Behler <i>et al.</i> (2018); Staniewicz <i>et al.</i> (2018)	Campbell (1972); Brazaitis & Watanabe (2011); Behler <i>et al.</i> (2018); Staniewicz <i>et al.</i> (2018)	
G	<i>Tomistoma schlegelii</i> (false gharial)	VU	Staniewicz <i>et al.</i> (2018)					Campbell (1972); Brazaitis & Watanabe (2011); Staniewicz <i>et al.</i> (2018)	Campbell (1972); Brazaitis & Watanabe (2011)	
G	<i>Gavialis gangeticus</i> (Indian gharial)	CR	McNeely & Sochaczewski (1991)						Campbell (1972); Brazaitis & Watanabe (2011)	

* 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.*, 2011*b*). 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.*, 2011*a*). 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.*, 2011*b*). 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.