

REVIEW

Frugivory and seed dispersal by crocodylians: an overlooked form of saurochory?

S. G. Platt¹, R. M. Elsey², H. Liu^{3,4}, T. R. Rainwater⁵, J. C. Nifong⁶, A. E. Rosenblatt⁷, M. R. Heithaus⁸ & F. J. Mazzotti⁹

1 Wildlife Conservation Society, Bronx, NY, USA

2 Louisiana Department of Wildlife and Fisheries, Rockefeller Wildlife Refuge, Grand Chenier, LA, USA

3 Department of Earth and Environment, Florida International University, Miami, FL, USA

4 Center for Tropical Plant Conservation, Fairchild Tropical Botanic Garden, Coral Gables, FL, USA

5 United States Fish and Wildlife Service, Charleston, SC, USA

6 Department of Biology, University of Florida, Gainesville, FL, USA

7 Department of Biological Sciences, Marine Sciences Program, Florida International University, Miami, FL, USA

8 School of Environment, Arts and Society, Florida International University, Miami, FL, USA

9 Department of Wildlife Ecology and Conservation, Fort Lauderdale Research and Education Center, University of Florida, Davie, FL, USA

Keywords

Alligator mississippiensis; Crocodylia; diet; foraging ecology; frugivory; saurochory; seed dispersal.

Correspondence

Thomas R. Rainwater, United States Fish and Wildlife Service, Charleston Field Office, 176 Croghan Spur Road, Suite 200, Charleston, SC 29407, USA
Email: trrainwater@gmail.com

Editor: Steven Le Comber

Received 19 December 2012; revised 1 May 2013; accepted 3 June 2013

doi:10.1111/jzo.12052

Abstract

Saurochory (seed dispersal by reptiles) among crocodylians has largely been ignored, probably because these reptiles are generally assumed to be obligate carnivores incapable of digesting vegetable proteins and polysaccharides. Herein we review the literature on crocodylian diet, foraging ecology, digestive physiology and movement patterns, and provide additional empirical data from recent dietary studies of *Alligator mississippiensis*. We found evidence of frugivory in 13 of 18 (72.2%) species for which dietary information was available, indicating this behavior is widespread among the Crocodylia. Thirty-four families and 46 genera of plants were consumed by crocodylians. Fruit types consumed by crocodylians varied widely; over half (52.1%) were fleshy fruits. Some fruits are consumed as gastroliths or ingested incidental to prey capture; however, there is little doubt that on occasion, fruit is deliberately consumed, often in large quantities. Sensory cues involved in crocodylian frugivory are poorly understood, although airborne and waterborne cues as well as surface disturbances seem important. Crocodylians likely accrue nutritional benefits from frugivory and there are no *a priori* reasons to assume otherwise. Ingested seeds are regurgitated, retained in the stomach for indefinite and often lengthy periods, or passed through the digestive tract and excreted in feces. Chemical and mechanical scarification of seeds probably occurs in the stomach, but what effects these processes have on seed viability remain unknown. Because crocodylians have large territories and undertake lengthy movements, seeds are likely transported well beyond the parent plant before being voided. Little is known about the ultimate fate of seeds ingested by crocodylians; however, deposition sites could prove suitable for seed germination. Although there is no evidence for a crocodylian-specific dispersal syndrome similar to that described for other reptiles, our review strongly suggests that crocodylians function as effective agents of seed dispersal. Crocodylian saurochory offers a fertile ground for future research.

Introduction

Seed dispersal by animals is a critical plant–animal mutualism that plays an important role in the demography, gene flow, distribution and evolution of plants (Howe & Smallwood, 1982; Jordano, 1992; Richardson, Brunsfeld & Klopfenstein,

2002a). While seed dispersal by insects, birds and mammals is well studied (Abrahamson, 1989; Schupp, Jordano & Gómez, 2010), saurochory, the dispersal of seeds by reptiles, has received comparatively little attention (Traveset, 1998) despite recognition that early reptiles were a significant selective force in the evolution of modern fruit (van der Pijl, 1982; Tiffney,

1986). Seed dispersal by aquatic and terrestrial chelonians (Moll & Jansen, 1995 and review therein; Varela & Bucher, 2002; Carlson, Menges & Marks, 2003; Ford & Moll, 2004; Liu, Platt & Borg, 2004; Graham & Sorrell, 2008; Stone & Moll, 2009; Kimmons & Moll, 2010), tuatara (Bredeweg & Nelson, 2010), lizards (Iverson, 1979; Whitaker, 1987; Fialho, 1990; Traveset, 1990; Valido & Nogales, 1994; Sáez & Traveset, 1995; Nogales, Delgado & Medina, 1998; Castilla, 1999; Hartley *et al.*, 2000; Valido, Nogales & Medina, 2003) and snakes (Mookerjee, 1946; Irvine, 1953; Engel, 1997) has been documented. However, saurochory by crocodylians has been largely overlooked, probably because these aquatic reptiles are generally assumed to be obligate carnivores (Lang, 1987) incapable of digesting vegetable proteins or polysaccharides (Neill, 1971; Coulson & Hernandez, 1983). This omission is somewhat surprising given that many carnivorous species of mammals and birds consume fruit, and are recognized as important primary and secondary seed dispersers (Darwin, 1859; Balgooyen & Moe, 1973; Herrera, 1988; Nogales *et al.*, 2002).

To better understand the potential role of crocodylians as seed dispersers, in this review, we pose the following questions: (1) Do crocodylians consume fruit and if so, how widespread is this behavior among the order Crocodylia? (2) If fruits are present in the diet, are these ingested incidental to prey capture, consumed as gastroliths, derived secondarily from ingested prey or deliberately ingested as food? (3) Does fruit consumption yield a nutritional reward for crocodylians? (4) What is the fate of fruits and seeds ingested by crocodylians? (5) Are movement patterns of crocodylians likely to extend the seed shadow much beyond the parent plant? (6) What are the ecological implications of this plant–animal interaction; that is, do crocodylians function as seed dispersers?

To answer these questions we reviewed the literature on crocodylian diet, foraging ecology, digestive physiology and movement patterns. In addition to our literature review, we revisited a Louisiana Department of Wildlife and Fisheries (LDWF) dataset used in an earlier study (McNease & Joanen, 1977) that consisted of stomach contents recovered from 314 American alligators (*Alligator mississippiensis*) harvested during 1972–1973 in Cameron Parish, Louisiana, USA. We also included data from two recent dietary studies of *Al. mississippiensis* conducted in Everglades National Park, Florida, USA, during June–November 2009 and October–November 2010 (A. E. Rosenblatt & M. R. Heithaus) and Sapelo Island, Georgia, USA, from March through November 2008–2010 (J. C. Nifong). Stomach contents in both studies (Everglades National Park; $n = 40$ and Sapelo Island; $n = 99$) were recovered by flushing (Taylor, Webb & Magnusson, 1978); J. C. Nifong also obtained stomach contents from a road-killed alligator and another that was euthanized after sustaining injuries in an aggressive intraspecific encounter.

Fruit consumption among the Crocodylia

We located dietary information for 18 of 23 extant species (Thorbjarnarson, 1992) of crocodylians. The number and

quality of dietary studies varies widely among the Crocodylia. The diet of some species (e.g. *Al. mississippiensis* and *Caiman crocodylus*) has been well studied in many parts of their respective geographic ranges, whereas other species are represented in the literature by few reports, many of which are based on small numbers of animals (e.g. Eaton & Barr, 2005; Pauwels *et al.*, 2007; Bezuijen, 2010), or consist of anecdotal observations of feeding behavior (e.g. Galdikas & Yeager, 1984). We found reports of fruits or seeds in the stomach contents or feces of 10 species (Table 1); three additional species (*Ca. latirostris*, *Al. sinensis* and *Crocodylus siamensis*) which are not included in this table have been observed consuming fruit in captivity and in the wild (Brito, Andrade & Abe, 2002; Brueggen, 2002; Dacey, 2012). Frugivory has thus been documented in 13 (72.2%) of 18 species for which dietary information is available. Frugivory was reported across size classes ranging from hatchlings to large adults.

Thirty-four families and 46 genera of plants were represented among seeds and fruits reportedly consumed by crocodylians (Table 2). Undoubtedly, this is a conservative assemblage as ‘unidentified’ seeds or fruits are listed in 13 (59.0%) of 22 dietary studies that report fruit consumption (Table 1). Fruit types consumed by crocodylians varied widely, and included fleshy aggregates (4), berries or berry-like fruits (10), capsules (2), nuts (4), nutlets (4), achenes (3), legumes (4), drupes (10), grains (4) and a cone (1). Notably, 24 (52.1%) of 46 identified fruits were fleshy fruits (aggregate, berry, drupe), which tend to be favored and dispersed by animals (Corlett, 1998; Hawthorne & Parren, 2000). Fruits ranged in size from grains (e.g. *Echinochloa*) and small nutlets (e.g. *Polygonum*) to large drupes (e.g. *Persea*, *Sacoglottis*).

We consider it likely that for several reasons, frugivory has either escaped detection or been underreported in dietary studies of crocodylians. First, the duration of many dietary studies is brief (<6 months), and sampling conducted outside of the fruiting period is unlikely to detect these seasonally available items (Leighton & Leighton, 1983). Second, if fruit consumption is infrequent, the apparent absence of fruit in the diet may simply be a consequence of the small number of animals sampled in some studies. Third and perhaps most importantly, because it is assumed that fruits make little energetic contribution to crocodylian diets (Neill, 1971; Coulson & Hernandez, 1983), those found in stomach contents or feces are considered anomalous and included in general categories such as ‘nonfood items’ (Platt *et al.*, 2006a), ‘vegetation’ (Thorbjarnarson, 1993b) or ‘plant material’ (McNease & Joanen, 1977), rather than being mentioned specifically. For example, McNease & Joanen (1977) stated only that ‘plant material’ occurred in 84.3% of 314 *Al. mississippiensis* stomachs examined, yet we found fruits or seeds of at least 16 species listed on the original data sheets (Table 1). Because seeds and fruits are often lumped into more inclusive categories, it is difficult to assess the prevalence of frugivory in most dietary studies. Based on the small number of studies in which specific information is provided on the presence of seeds and fruits in the diet, frugivory appears to occur frequently in at least some crocodylian populations (Table 3).

Table 1 Fruits and seeds reported in stomach contents and feces of crocodilians

Species	Source	Fruit or seeds
<i>Alligator mississippiensis</i>	Dowler (1846)	<i>Gossypium</i> sp.
	Anonymous (1878)	<i>Rubus</i> sp.
	Kellogg (1929)	<i>Carya</i> sp.
	Valentine <i>et al.</i> (1972)	Unidentified seeds
	Platt <i>et al.</i> (1990)	<i>Taxodium distichum</i> ; <i>Vigna luteola</i> .
	Forkner (1996)	<i>Carya</i> sp.; <i>Juglans nigra</i> .
	Rice (2004)	Unidentified seeds and nuts
	Saalfeld (2010)	Unidentified seeds
	LDWF (this study)	<i>Asimina triloba</i> , <i>Brasenia schreberi</i> , <i>Cladium jamaicense</i> , <i>Daubentonia</i> sp., <i>Eleocharis</i> sp., <i>Heliotropium</i> sp., <i>Hydrochloa carolinensis</i> , <i>Ipomoea</i> sp., <i>Limnobiium spongia</i> , <i>Melia azedarach</i> , <i>Orzya sativa</i> , <i>Passiflora incarnata</i> , <i>Phaseolus</i> sp., <i>Polygonum</i> sp., <i>Sesbania macrocarpa</i> ; unidentified seeds.
	Nifong (this study)	<i>Echinochloa</i> sp., <i>Juniperus virginiana</i> , Leguminosae, <i>Melia azedarach</i> , <i>Myrica</i> sp., <i>Nelumbo lutea</i> , <i>Nyssa sylvatica</i> , <i>Quercus laurifolia</i> , <i>Sabal palmetto</i> , <i>Serenoa repens</i> , unidentified seeds.
<i>Caiman crocodilus</i>	Rosenblatt (this study)	<i>Annona glabra</i> ; <i>Chrysobalanus icaco</i> , <i>Rhizophora mangle</i> .
	Staton & Dixon (1975)	Unidentified seeds
<i>Crocodylus acutus</i>	Thorbjarnarson (1993a)	Unidentified seeds
	Casas-Andreu & Quiroz (2003)*	Unidentified seeds
<i>Crocodylus cataphractus</i>	Platt <i>et al.</i> (2013)	<i>Byrsonima crassifolia</i>
	Mazzotti (this study)	<i>Rhizophora mangle</i>
<i>Crocodylus moreletii</i>	Eaton & Barr (2005)	Unidentified Palmae
<i>Crocodylus niloticus</i>	Platt <i>et al.</i> (2002, 2006a)	Unidentified seeds
	Schmidt (1924)	Unidentified nutlet
<i>Crocodylus palustris</i>	Wallace & Leslie (2008)	<i>Cyperus papyrus</i>
<i>Crocodylus porosus</i>	D'Abreu (1915)	<i>Oryza</i> sp.
<i>Osteolaemus tetraspis</i>	Webb & Manolis (1989)	Unidentified seeds
<i>Paleosuchus trigonatus</i>	Pauwels <i>et al.</i> (2007)	<i>Sacoglottis gabonensis</i> ; unidentified fruits.
	Vanzolini & Gomes (1979)	Unidentified seeds

Asterisk denotes study based on fecal analyses. LDWF, Louisiana Department of Wildlife and Fisheries.

Another difficulty encountered when attempting to assess the importance of fruit in the diet is that even when the occurrence of frugivory is specifically noted, the quantity of propagules recovered is usually not reported. However, a handful of accounts collectively suggest that individual crocodilians at least occasionally ingest significant numbers of fruits. A peck (c. 9.0 L) of *Rubus* fruit (945 fruits assuming 105 fruits/L) were found in the stomach of an adult *Al. mississippiensis* (Anonymous, 1878), and the stomach of another adult contained a peck of *Gossypium* seeds (Dowler, 1846); given that each capsule contains 12 to 16 small seeds (Standley, 1961), the presence of so many seeds in a single stomach indicates that a large number of fruits were consumed. According to Forkner (1996), the stomach of an alligator yielded a 'large quantity' of *Juglans nigra* and *Carya* spp. nuts. Captive *Al. mississippiensis* and *Ca. latirostris*, respectively, consumed complete panicles of *Sambucus canadensis* fruit (Brueggen, 2002), and 'multiple' *Philodendron selloum* fruits (Brito *et al.*, 2002). The stomachs of *Cr. moreletii* hatchlings contained up to six unidentified seeds (Platt, Rainwater & McMurry, 2002). Fruit was found in the stomachs of two *Osteolaemus tetraspis*; one contained a single *Sacoglottis gabonensis* fruit and two unidentified fruits were recovered from the other (Pauwels *et al.*, 2007). Unpublished LDWF data and recent dietary

studies of *Al. mississippiensis* found considerable numbers of some seeds present in stomachs (Table 4). Given the gastric capacity of large adults (Chabreck, 1972; Richardson, Webb & Manolis, 2002b), crocodilians would seem capable of ingesting significant numbers of fruits; although this is not apparent in most reports of frugivory.

Fruit ingestion by crocodilians

Unlike studies of mammalian and avian frugivory, which are often based on direct observation of foraging individuals, most evidence for crocodilian frugivory is inferred from the presence of seeds and fruits among stomach contents and to a much lesser extent, feces. Because analyses of stomach contents and feces reveal only the composition of the diet and not the foraging mode (DeVault & Rhodes, 2002), it is possible the presence of fruits and seeds result from behaviors and processes other than deliberate consumption as food. Diefenbach (1979) suggested that nonfood objects such as stones (and presumably fruits and seeds) might be accidentally ingested as crocodilians forage for aquatic gastropods and other prey among bottom sediments and debris. Brito *et al.* (2002) speculated that fruit is accidentally ingested by crocodilians attempting to capture associated insects.

Table 2 Fruits consumed by crocodilians

Family	Species	Fruit type	Fruit color
Annonaceae	<i>Anona glabra</i>	Fleshy aggregate	Yellow
	<i>Asimina triloba</i>	Fleshy aggregate	Black
Araceae	<i>Philodendron selloum</i>	Berry	White-yellow
Arecaceae	<i>Sabal palmetto</i>	Drupe	Black
	<i>Serenoa repens</i>	Drupe	Black
Boraginaceae	<i>Heliotropium</i> sp.	Nutlet	Blue
Cabombaceae	<i>Brasenia schreberi</i>	Nutlet	Green-yellow
Cactaceae	<i>Opuntia</i> spp.	Berry	Red-purple
Caprifoliaceae	<i>Sambucus canadensis</i>	Berry	Purple
Chrysobalanaceae	<i>Chrysobalanus icaco</i>	Drupe	Pink-white
Convolvulaceae	<i>Ipomoea</i> sp.	Capsule	Green-brown
Cucurbitaceae	<i>Citrullus lanatus</i>	Berry	Green
	<i>Cucurbita</i> spp.	Berry	Yellow-orange
	<i>Juniper virginiana</i>	Berry-like	Blue-black
Cyperaceae	<i>Cladium jamaicense</i>	Achene	Brown
	<i>Eleocharis</i> sp.	Achene	Brown
	<i>Cyperus papyrus</i>	Achene	Brown
Fabaceae	<i>Daubentonia</i> sp.	Legume	Green
	<i>Phaseolus</i> sp.	Legume	Green
	<i>Sesbania macrocarpa</i>	Legume	Green
	<i>Vigna luteola</i>	Legume	Green
Fagaceae	<i>Quercus</i> sp.	Nut	Brown
	<i>Q. laurifolia</i>	Nut	Brown
Humiriaceae	<i>Sacoglottis gabonensis</i>	Drupe	Black
Hydrocharitaceae	<i>Limnobium spongia</i>	Berry	Green
Juglandaceae	<i>Carya</i> spp.	Nut	Brown
	<i>Juglans nigra</i>	Nut	Brown
	<i>Persea americana</i>	Drupe	Black-green
Malpighiaceae	<i>Byrsonima crassifolia</i>	Drupe	Yellow-orange
Malvaceae	<i>Gossypium</i> spp.	Capsule	Green-brown
Meliaceae	<i>Melia azedarach</i>	Drupe	Yellow-orange
Moraceae	<i>Ficus racemosa</i>	Fleshy aggregate	Red
Myricaceae	<i>Myrica</i> sp.	Drupe	White
Nelumbonaceae	<i>Nelumbo lutea</i>	Nut-like	Black
Nyssaceae	<i>Nyssa</i> sp.	Drupe	Blue
Palmae	NA	Drupe	
Passifloraceae	<i>Passiflora incarnata</i>	Berry	Green
Poaceae	<i>Echinochloa</i> sp.	Grain	Brown
	<i>Hydrochloa caroliniensis</i>	Grain	Brown
	<i>Oryza sativa</i>	Grain	Brown
	<i>Zea mays</i>	Grain	Purple-red-yellow
Polygonaceae	<i>Polygonum</i> spp.	Nutlet	Brown
Rhizophoraceae	<i>Rhizophora mangle</i>	Berry-like	Red-brown
Rosaceae	<i>Rubus</i> spp.	Fleshy aggregate	Red-black
Rutaceae	<i>Citrus</i> spp.	Berry	Yellow-orange
Vitaceae	<i>Vitis</i> spp.	Berry	Red-purple
Taxodiaceae	<i>Taxodium distichum</i>	Cone	Brown

Inclusion based on fruits or seeds found in stomach contents and feces, and foraging observations of wild and captive crocodilians. NA, not available; species not identified in original account. Taxonomy, fruit type and color follows Standley (1961), Kunkel (1965), Mors & Rizzini (1966), Radford & Bell (1968), Godfrey & Wooten (1979) and Elias (1987).

According to Webb & Manolis (1989), floating fruits might be consumed when mistaken for aquatic insects by crocodilians. Furthermore, for reasons yet unknown, crocodilians occasionally ingest large amounts of vegetation (Supporting Information Appendix S1), and undoubtedly ingest fruits

and seeds at the same time. Ingestion of foliage with accompanying fruits and seeds is consistent with the 'foliage as fruit hypothesis' proposed by Janzen (1984); foliage of small-seeded plants can function ecologically as fruit, attracting herbivores just as fleshy fruits attract and reward frugivores.

Table 3 Frequency of occurrence (%) of frugivory reported in dietary studies of crocodylians

Species	<i>n</i>	%	Source
<i>Alligator mississippiensis</i>	314	8.5	LDWF (this study)
	99	40.4	Nifong (this study)
	40	25.0	Rosenblatt (this study)
<i>Caiman crocodylus</i>	274	14.3	Thorbjarnarson (1993a)
<i>Crocodylus acutus</i>	56*	21.4	Casas-Andreu & Quiroz (2003)
<i>Crocodylus cataphractus</i>	2	50.0	Eaton & Barr (2005)
<i>Crocodylus moreletii</i>	71	2.8	Platt <i>et al.</i> (2002)
<i>Osteolaemus tetraspis</i>	22	9.0	Pauwels <i>et al.</i> (2007)

n, number of stomachs flushed or feces examined (asterisk denotes fecal samples). LDWF, Louisiana Department of Wildlife and Fisheries.

Table 4 Quantity of seeds found in the stomachs of American alligators (*Alligator mississippiensis*) from southwestern Louisiana, Sapelo Island, Georgia and Everglades National Park, Florida

Species	<i>n</i>	No. of seeds or range
<i>Annona glabra</i>	7	1–1286
<i>Asimina triloba</i>	1	4
<i>Brasenia schreberi</i>	1	1
<i>Chrysobalanus icaco</i>	2	1–6
<i>Cladium jamaicense</i>	3	20–46
<i>Daubentonia</i> sp.	1	1
<i>Eleocharis</i> sp.	1	2
<i>Helitropium</i> sp.	2	225–400
<i>Hydrochloa carolinensis</i>	1	'Many'
<i>Ipomea</i> sp.	1	1
<i>Juniperus virginiana</i>	4	1–3
<i>Limnobiium spongia</i>	1	3
<i>Melia azedarach</i>	5	1–17
<i>Myrica</i> sp.	1	1
<i>Nyssa sylvatica</i>	1	3
<i>Orzya sativa</i>	1	4
<i>Passiflora incarnata</i>	3	1–204
<i>Phaseolus</i> sp.	1	6
<i>Polygonum</i> sp.	3	42–294
<i>Quercus laurifolia</i>	3	1
<i>Rhizophora mangle</i>	1	2
<i>Sabal palmetto</i>	5	3–61
<i>Serenoa repens</i>	5	1–10
<i>Sesbania macrocarpa</i>	2	1

n, number of stomachs containing a particular food item.

Additionally, crocodylians actively seek out and ingest stones and other objects that act as gastroliths (Peaker, 1969; Fitch-Snyder & Lance, 1993), and hard seeds might also serve this purpose (Staton & Dixon, 1975; Platt *et al.*, 2002), particularly in substrates where stones are rare or absent (Platt, Brantley & Hastings, 1990).

Fruits and seeds found in stomach contents and feces could also result from secondary ingestion; that is, the acquisition of items contained in the gut of primary prey (Cott, 1961). Crocodylians are generalist predators that consume prey ranging in size from small invertebrates to large mammals,

including carrion (Pooley, 1989; Kofron, 1993; Platt *et al.*, 2007). This diverse array of prey includes many herbivorous, frugivorous and granivorous species; hence, numerous opportunities exist for crocodylians to ingest fruits and seeds already present in the gut of their prey, and to function as secondary seed dispersers (Nogales *et al.*, 1998). We are unaware of any report in which propagules found in the stomach contents or feces of crocodylians could be unequivocally attributed to secondary ingestion. However, when revisiting data used by McNease & Joanan (1977), we noted that 10 (38.4%) of 26 *Al. mississippiensis* stomachs containing seeds or fruits also contained the remains of boat-tailed grackles (*Quiscalus major*; four stomachs), red-winged blackbirds (*Agelaius phoeniceus*; five stomachs) and a goose (probably *Branta canadensis*; one stomach). Similarly, raccoon (*Procyon lotor*) remains were found in two stomachs also containing seeds (A. E. Rosenblatt, pers. obs.). Because these birds all include fruits and seeds in their diet (Ehrlich, Dobkin & Wheye, 1988) and frugivory by raccoons is well documented (Zevloff, 2002), we concede that secondary ingestion could account for at least some seeds and fruit found in these studies, and probably others as well.

Reports of accidental and secondary ingestion notwithstanding, observations of captive and wild crocodylians indicate that on occasion, fruits are deliberately consumed, apparently as food. In captivity, *Ca. latirostris* were observed feeding on *Philodendron selloum* fruit from plants growing in their enclosure (Brito *et al.*, 2002). Likewise, *Al. mississippiensis* consumed wild grape (*Vitis* spp.), elderberry (*Sambucus canadensis*) and citrus (*Citrus* spp.) fruits directly from trees, and foraged below citrus trees for fallen fruits (Brueggen, 2002). Both *Al. mississippiensis* and *Al. sinensis* consumed squash (*Cucurbita* spp.) provided for tortoises (Testudinidae) sharing the same enclosure (Brueggen, 2002).

Observations of fruit consumption in the wild are less common, which is unsurprising given that crocodylians can be wary and difficult to observe, much foraging is nocturnal, and aquatic vegetation and turbidity often obscure foraging activity (Magnusson, Silva & Lima, 1987; Thorbjarnarson, 1993b). Indeed, there is a notable paucity of information on foraging behaviors associated with the ingestion of even commonly consumed prey (Gans, 1989). Nonetheless, a scattering of reports indicate that deliberate frugivory occurs among wild crocodylians. According to Morelet (1871), 'alligators' (undoubtedly *Cr. moreletii* given the geographic location of this account) are 'very fond' of *Persea americana* fruit, accounting 'for the name alligator pear, which has been bestowed upon it'. In Belize, the vernacular name 'alligator-pear' is applied to *Annona glabra* and according to villagers, *Cr. moreletii* and possibly *Cr. acutus* consume the fruit (S. G. Platt & T. R. Rainwater, pers. obs.). Elsewhere in the Neotropics, *An. glabra* is known as 'alligator-apple' owing to the affinity of crocodylians for its fruit (Guppy, 1917; Ridley, 1930; Standley, 1961). Abdulali (1938) observed *Cr. palustris* eating fallen *Ficus glomerata* (*racemosa*) fruit, Dacey (2012) watched an adult *Cr. siamensis* consume *Citrullus lanatus*, and one of us (F. J. Mazzotti)

observed *Cr. acutus* consuming propagules of *Rhizophora mangle*. *Al. mississippiensis* reportedly consume the fruit of *Opuntia* (Vosburgh, 1949) and *Cucurbita* (Foster, 1998), and have been photographed with motion-sensitive trail cameras eating *Zea mays* dispensed by automatic wildlife feeders (Platt & Elsey, 2011).

It remains unclear what sensory cues are involved in crocodilian frugivory. Fruit color can serve as an important signal of both fruit presence and fruit maturity (Lambert & Garber, 1998), although discussion of color is complicated by the fact that human color vision is not typical of most vertebrates (Tovée, 1995; Corlett, 1998). The presence of photosensitive pigments in the crocodilian retina that respond over the 400–700 nm spectrum suggests colors can be discriminated (Richardson *et al.*, 2002b), but whether color plays any role in foraging behavior is unknown. Given the range of colors among fruits exploited by crocodilians (Table 2), color does not seem to be the primary factor in fruit selection and other cues are probably involved. Airborne and waterborne chemical cues are used to locate animal prey (Scott & Weldon, 1990; Weldon *et al.*, 1990), and could likewise play a similar role in frugivory. Crocodilians are attracted to surface disturbances (Brazaitis, 1969; Hartley & Hartley, 1977; Lazell & Spitzer, 1977) perceived through unique sensory receptors on the face (Soares, 2002), and falling fruit hitting the water could elicit a feeding response in the same manner as suggested for fish (Correa *et al.*, 2007). Unfortunately, the available reports of crocodilian frugivory provide little insight into how crocodilians detect fruits prior to consumption.

Nutritional benefits of frugivory to crocodilians

Animal-mediated seed dispersal is often a mutualistic interaction between plants and their dispersers; the disperser transports propagules out of the seed shadow of the parent plant, and in turn receives a nutritional reward of energy-rich fruit (Herrera, 2002). Early research suggested that like many obligate carnivores, crocodilians were unable to metabolize dietary carbohydrates and other plant-based nutrients (Coulson & Hernandez, 1983). However, subsequent work with *Al. mississippiensis* demonstrated crocodilians are capable of digesting carbohydrates, plant-based proteins and vegetable fats (Coulson *et al.*, 1987; Staton, 1988), and supplementing high-protein diets with carbohydrates increased both food conversion efficiency and growth (Staton *et al.*, 1990; Smith & Coulson, 1992). Furthermore, measurable levels of amylolytic enzymes, which hydrolyze carbohydrates for absorption into the bloodstream, have been found in the duodenal and pancreatic tissue of *Cr. porosus* (Read & Anderson, 2000). Thus, there is no *a priori* reason for assuming crocodilians consume fruit for reasons other than nutrition. While much remains to be learned about how crocodilians process carbohydrates and other plant-based nutrients, collectively, these studies suggest that frugivory is likely to yield nutritional rewards for crocodilians.

The fate of fruits and seeds ingested by crocodilians

Crocodilians do not masticate food; instead, prey items are grasped with the teeth, positioned in the mouth by a series of inertial bites, moved into the rear of the oral cavity and swallowed (Cleuren & De Vree, 2000). Prey size is limited primarily by gape size, and consequently, crocodilians are capable of ingesting relatively large items (Cleuren & De Vree, 2000). Given the mechanics of ingestion, most fruits are probably intact upon entering the stomach, and then rapidly digested in the highly acidic (pH = 1.2 to 2.0) gastric environment (Diefenbach, 1975b; Coulson, Herbert & Coulson, 1989) leaving only the seeds. While fate of seeds in the digestive system has not been specifically investigated, inferences can be made based on other hard objects ingested by crocodilians. Digestive seed predation is one possible outcome of frugivory as some seeds, particularly caryopses and nuts (e.g. Kellogg, 1929) are crushed by the muscular action of the stomach wall acting in concert with gastroliths such as small stones (Sokol, 1971; Davenport *et al.*, 1990). However, most reports indicate that seeds are intact when recovered, suggesting these items are treated by the digestive system similar to other indigestible items, which are either regurgitated (nonconvulsive oral voiding distinguished from convulsive vomiting; Diefenbach, 1981), passed through the digestive tract or retained in the stomach for indefinite and often lengthy periods (Richardson *et al.*, 2002b).

Hairballs, feathers, snail opercula and other indigestible objects too large to pass through the pyloric orifice are regurgitated, often encased in a compact bolus of hair (Diefenbach, 1981; Fisher, 1981; Chabreck, 1996); large seeds could be treated likewise, although regurgitation of seeds has never been documented. Smaller indigestible objects are excreted in feces (Diefenbach, 1981; Chabreck, 1996), an organic matrix largely consisting of decalcified prey remains (Fisher, 1981). Seeds have been recovered from the feces of *Cr. acutus* (Casas-Andreu & Quiroz, 2003), apparently the only report describing the post-digestive fate of seeds or fruits. This is likely due in part to the fact that fecal analyses have rarely been used to investigate crocodilian diet (but see Whitaker & Whitaker, 1984; Shoop & Ruckdeschel, 1990; Bezuijen, 2010), perhaps because feces are infrequently encountered and difficult for researchers to find in the wild (S. G. Platt, T. R. Rainwater & R. M. Elsey, pers. obs.).

Gastric residence time for ingested items is highly variable and depends on temperature, meal size, food consumption rate and composition of the food (Diefenbach, 1975b; McWilliams, Afik & Secor, 1997; Janes & Gutzke, 2002). Most items remain in the stomach for 24 to 45 h and pass through the entire digestive tract in 4–5 days (Davenport *et al.*, 1990), a gut passage rate comparable to many birds and larger mammals (Willson, 1993). Laxative compounds in fruits could potentially reduce gastric residence time by increasing defecation frequency (Murray *et al.*, 1994), but these effects have not been investigated in crocodilians (or any other reptiles). On the other hand, some indigestible objects that are neither regurgitated nor excreted in feces remain in

the stomach much longer, although this aspect of the digestive process is poorly understood. Garnett (1985) found small fragments of chitin remained in the stomach for 5 months before being recovered by stomach flushing. Delaney *et al.* (2011) reported that after 588 days, 76% of metal tags experimentally fed to a group of captive alligators had yet to be eliminated from the stomach. Of the tags that were eliminated, the first were passed between 46 and 106 days post-ingestion. Others have likewise noted the long-term accumulation of indigestible items in the stomach, but concluded these must eventually be regurgitated or excreted because gastric capacity is limited (Diefenbach, 1981; Horna, Cintra & Ruesta, 2001).

During the period seeds reside in the stomach, the seed coat is likely to be chemically scarified by gastric acids (Coulson *et al.*, 1989) and mechanically abraded by gastroliths (Bakker, 1971; Diefenbach, 1975a). What effect these processes might have on seed survival in the stomach and subsequent germination has yet to be investigated in crocodylians. In general, seed survival is a function of gastric residence time, declining the longer a seed remains in the stomach (Janzen, 1981, 1982). Post-digestion germination experiments comparing seeds collected from crocodylian feces (or regurgitate) with those harvested directly from plants are notably absent from the literature (Traveset, 1998).

Other considerations

In addition to the type and quantity of fruit ingested, mechanics of ingestion and the effects of gut passage on seeds, other variables that must be considered when evaluating dispersal effectiveness include dispersal distance and the quality of deposition (Schupp *et al.*, 2010). Seed transport by dispersers facilitates escape from the parent plant, and for a variety of reasons, the likelihood of post-dispersal seedling survival is greater with increasing dispersal distance (Howe & Smallwood, 1982; Howe & Miriti, 2004), which in turn is largely determined by the ranging behavior of the disperser (Corlett, 1998).

Crocodylians exhibit complex movement patterns that vary depending on sex, age, body size, reproductive status and season (Hutton, 1989; Rootes & Chabreck, 1993; Tucker *et al.*, 1997, 1998), even among individuals of the same sex and similar body size (Rosenblatt & Heithaus, 2011). Adult crocodylians establish and defend territories (Lang, 1987) that can encompass hundreds to thousands of hectares (up to 5000 ha in some populations of *Al. mississippiensis*; Joanen & McNease, 1972), and daily movements within these territories can be extensive. For example, adult *Gavialis gangeticus* in a large river reportedly moved 12 km in 2 h (Bustard & Singh, 1983). Male *Cr. porosus* moved an average of 4.0 km d⁻¹ during the dry season, and the greatest distance moved during a single day was 23.3 km (Kay, 2004). Similarly, several adult *Al. mississippiensis* moved at least 13.4 km in a single day (Rosenblatt & Heithaus, 2011), and an adult female moved 24.9 km in 68 days (2.7 km d⁻¹; Lance *et al.*, 2011). Favorable currents appear to facilitate long-distance movements of crocodylians in river systems (Kay, 2004). In at least one species (*Cr. porosus*), long-distance oceanic voyages

between widely separated island populations occur regularly (Campbell *et al.*, 2010). Although nothing quantitative is known about seed shadows generated by crocodylians, their complex and often extensive movements coupled with the potentially lengthy gastric residence periods of seeds could result in long-distance seed dispersal with attendant consequences for the spatial distribution of plants (Cain, Milligan & Strand, 2000).

Quality of deposition refers to the probability that a seed will survive ingestion in a viable condition, be deposited at a site suitable for germination and survive to produce a new adult (Schupp *et al.*, 2010). Although locations of suitable deposition sites are unpredictable, some sites are predictably associated with higher probabilities of seedling survival in comparison to others (Schupp *et al.*, 1989). The biotic and physical conditions of the deposition site are primarily determined by attributes of the disperser (Schupp, 1993). Very little is known concerning the deposition of seeds ingested by crocodylians. Regurgitation of indigestible items by captive crocodylians takes place in the water (Diefenbach, 1981), and presumably occurs likewise in the wild, although observations are lacking. Similarly, the defecation habits of wild crocodiles are poorly documented. *Cr. moreletii* deposits feces at basking sites and underwater (S. G. Platt & T. R. Rainwater, pers. obs.). *Al. mississippiensis* feces have been found on top of nest mounds (R. M. Elsey, pers. obs.), which consist of soil and decomposing vegetation (McIlhenny, 1935), and atop levees separating wetland habitats (T. R. Rainwater & P. M. Wilkinson, pers. obs.). Casas-Andreu & Quiroz (2003) recovered *Cr. acutus* feces at basking sites, and *Cr. siamensis* feces were found along seasonally exposed lake margins and on mats of floating vegetation (Platt *et al.*, 2006b; Bezuijen, 2010). Whether these locations constitute suitable germination sites is speculative, but mounds of soil and decomposing vegetation, exposed moist soil along lake margins and floating organic mats would seem to provide adequate conditions for seed germination. Crocodylians often inhabit seasonally flooded wetlands, and seeds deposited underwater might be exposed by falling water levels and germinate during the dry season. Seeds deposited in streams or rivers could also be secondarily dispersed by water currents in the same manner suggested for semi-aquatic mammals that often defecate underwater (Crawley, 1983; Beck-King, von Helverson & Beck-King, 1999). Furthermore, the accumulation of crocodylian dung at frequently used basking sites creates nutrient 'hot spots' (Rosenblatt & Heithaus, 2011) that could prove favorable for seedling establishment and growth. Sites where seed-filled dung accumulates often have consistent, disproportionately high, seedling recruitment over time (Russo & Augspurger, 2004).

Conclusions and future directions

Despite significant gaps in our knowledge of crocodylian foraging ecology, diet and nutritional physiology, several facts emerge from our review. Foremost is that although under-reported, frugivory appears widespread among the Crocodylia. Some frugivory is certainly attributable to accidental

or secondary ingestion, and ingestion of fruits and seeds when consuming vegetation, but the literature leaves little doubt that on occasion, crocodilians deliberately eat fruit. Crocodilians are probably best considered 'occasional frugivores' (*sensu* Willson, 1993), that is, generalist predators that complement an otherwise carnivorous diet with fruit, which is consumed infrequently and usually, but not always in small quantities. Although fruit seems of limited importance in crocodilian diets, nutritional benefits likely accrue from frugivory.

The diversity of fruit types consumed by crocodilians seems to preclude the existence of a specific crocodilian dispersal syndrome similar to that described for other reptiles (aromatic, colorful fruits, borne at ground level or dropped at maturity) by van der Pijl (1982). Nonetheless, several lines of evidence strongly suggest that crocodilians potentially function as effective agents of seed dispersal. Crocodilians are capable of ingesting large numbers of fruits and seeds, and because these are swallowed without mastication, seeds are likely to escape damage during ingestion. Among birds and mammals, seeds ingested by 'swallowers' have a greater probability of being successfully dispersed relative to other modes of fruit consumption (Schupp, 1993). Moreover, the expansive gape capacity of crocodilians permits the ingestion of large-seeded fruits (e.g. *S. gabonensis*, *P. americana* and perhaps some *Palmae*), a group constrained by access to a limited suite of vertebrate dispersers (Corlett, 1998; Peres, 2000). Once ingested, the fate of seeds is less clear; while digestive predation of some seeds undoubtedly occurs, most are probably regurgitated or excreted in the feces. What effects digestive processes have on seed viability remains unknown, and the potentially long gastric residence times are cause for concern. Because crocodilians have large territories and frequently undertake lengthy movements, they are capable of generating extensive seed shadows; seeds are transported well beyond the parent plant before being voided. Although little is known about the ultimate deposition of seeds ingested by crocodilians, the few available reports suggest that defecation sites could prove suitable for seed germination.

Admittedly, many of our conclusions are tentative and often speculative, and much remains to be learned about crocodilian saurochory; however, our review suggests a fertile ground for future research. Most importantly, the occurrence of seeds and fruits among stomach contents and feces should henceforth be considered evidence of possible frugivory rather than consigned to the dustbin of generalized dietary categories. Furthermore, a better understanding of the fate of ingested seeds is urgently needed to assess crocodilian saurochory. Are seeds regurgitated or deposited in the feces, and how long do these items remain in the digestive tract? Basic information on the defecation habits of crocodilians would go far toward understanding the likelihood of post-digestive seedling survival. To this end, germination experiments comparing seeds ingested by crocodilians with others harvested directly from plants are recommended. Such experiments are essential to quantify important components of disperser effectiveness (germinability, survivorship and dormancy periods of ingested seeds), but are seldom performed in studies of saurochory (Willson, 1993; Liu *et al.*, 2004). Because croc-

odilian foraging ecology is difficult to study in wild populations, many of these questions are probably best addressed using captive animals. Given the biomass of crocodiles in many subtropical and tropical wetlands (Platt *et al.*, 2009, 2011; Fukuda *et al.*, 2011), their capacity for ingesting large numbers of fruits, and the unspecialized, diffuse nature of many seed dispersal mutualisms (Wheelwright & Orians, 1982; Herrera, 1985; Howe, 1985), we consider it likely that crocodilians function as significant seed dispersal agents in many freshwater ecosystems.

Acknowledgments

Studies conducted by J. Nifong on Sapelo Island, Georgia, were supported in part by NSF grant numbers OCE-9982133 and OCE-0620959, and alligator stomach contents were taken under Georgia Department of Natural Resources Collecting Permit 29-WBH-0956 and University of Florida IACUC Protocol 201005071. Research on alligators by A. Rosenblatt, M. Heithaus and F. Mazzotti was funded by the Florida Coastal Everglades Long-Term Ecological Research Program under NSF Grant number DEB-9910514, and performed under Everglades National Park Permits EVER-2009-SCI-0024 and EVER-2011-SCI-0031 and Florida International University IACUC Protocol 09-013. Scott Zona assisted with the identification of seeds collected by Rosenblatt. We are grateful to Madeline Thompson and Kent Vliet for providing a number of obscure references. Conversations with John Brueggen and John Thorbjarnarson sparked our interest in crocodilian frugivory and seed dispersal. Comments by Lewis Medlock greatly improved an early draft of our paper. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service. We dedicate this paper to our friend and colleague, John B. Thorbjarnarson (1957–2010), in recognition of a life devoted to the study and conservation of crocodilians.

References

- Abdulali, H. (1938). The food of the mugger (*Crocodilus palustris*). *J. Bombay Nat. Hist. Soc.* **40**, 336.
- Abrahamson, W.G. (1989). *Plant–animal interactions*. New York: McGraw-Hill.
- Anonymous. (1878). An alligator's meal. *Chicago Daily Tribune*, 23 June, page 3.
- Bakker, R.T. (1971). Ecology of the brontosaurus. *Nature* **229**, 172–174.
- Balgooyen, T.G. & Moe, L.M. (1973). Dispersal of grass fruits – an example of endornithochory. *Am. Midl. Nat.* **90**, 454–455.
- Beck-King, H., von Helverson, O. & Beck-King, R. (1999). Home range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: a study using alternative methods. *Biotropica* **31**, 675–685.
- Bezuijen, M.R. (2010). *Crocodylus siamensis* (Siamese crocodile). *Diet. Herpetol. Rev.* **41**, 68–69.
- Brazaitis, P. (1969). The occurrence and ingestion of gastroliths in two captive crocodilians. *Herpetologica* **25**, 63–64.

- Bredeweg, E.M. & Nelson, N.J. (2010). *Sphenodon punctatus* (Tuatara). Frugivory. *Herpetol. Rev.* **41**, 211–212.
- Brito, S.P., Andrade, D.V. & Abe, A.S. (2002). Do caimans eat fruit? *Herpetol. Nat. Hist.* **9**, 95–96.
- Brueggen, J. (2002). Crocodylians eating their vegetables. *IUCN Croc. Special Group Newsl.* **21**, 16.
- Bustard, H.R. & Singh, L.A.K. (1983). Movement of wild gharial, *Gavialis gangeticus* (Gmelin) in the River Mahanadi, Orissa (India). *Br. J. Herpetol.* **6**, 287–291.
- Cain, M.L., Milligan, B.G. & Strand, A.E. (2000). Long-distance seed dispersal in plant populations. *Am. J. Bot.* **87**, 1217–1227.
- Campbell, H.A., Watts, M.E., Sullivan, S., Read, M.A., Choukroun, S., Irwin, S.R. & Franklin, C.E. (2010). Estuarine crocodiles ride surface currents to facilitate long-distance travel. *J. Anim. Ecol.* **79**, 955–964.
- Carlson, J.E., Menges, E.S. & Marks, P.L. (2003). Seed dispersal by *Gopherus polyphemus* at Archbold Biological Station, Florida. *Fla. Sci.* **66**, 147–154.
- 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, México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología* **74**, 35–42.
- Castilla, A.M. (1999). *Podarcis lilfordi* from the Balearic islands as a potential disperser of the rare Mediterranean plant *Withania frutescens*. *Acta Oecol.* **20**, 119–124.
- Chabreck, R.H. (1972). The foods and feeding habits of alligators from fresh and saline environments in Louisiana. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* **25**, 117–124.
- Chabreck, R.H. (1996). Regurgitation by the American alligator. *Herpetol. Rev.* **27**, 185–186.
- Cleuren, J. & De Vree, F. (2000). Feeding in crocodylians. In *Feeding: form, function, and evolution in tetrapod vertebrates*: 337–358. Schwenk, K. (Ed.). San Diego: Academic Press.
- Corlett, R.T. (1998). Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biol. Rev.* **73**, 413–448.
- Correa, S.B., Winemiller, K.O., Lopez-Fernandez, H. & Galetti, M. (2007). Evolutionary perspectives on seed consumption and dispersal by fishes. *Bioscience* **57**, 748–756.
- Cott, H.B. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and northern Rhodesia. *Trans. Zool. Soc. Lond.* **29**, 211–357.
- Coulson, R.A., Coulson, T.D., Herbert, J.D. & Staton, M.A. (1987). Protein nutrition in the alligator. *Comp. Biochem. Physiol.* **87A**, 449–459.
- Coulson, R.A., Herbert, J.D. & Coulson, T.D. (1989). Biochemistry and physiology of alligator metabolism *in vivo*. *Am. Zool.* **29**, 921–934.
- Coulson, T.D. & Hernandez, T. (1983). *Alligator metabolism: studies on chemical reactions in vivo*. New York: Pergamon Press.
- Crawley, M.J. (1983). *Herbivory: the dynamics of animal–plant interactions*. Berkeley: University of California Press.
- D’Abreu, E.A. (1915). Note on the ‘mugger’ *Crocodylus palustris*; contents of their stomachs, folklore, etc. *J. Bombay Nat. Hist. Soc.* **23**, 780.
- Dacey, T. (2012). Summary report on a visit to Lao PDR. *IUCN Croc. Spec. Group Newsl.* **31**, 6–8.
- Darwin, C. (1859). *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. London: John Murray.
- Davenport, J., Grove, D.J., Cannon, J., Ellis, T.R. & Stables, R. (1990). Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus*. *J. Zool. (Lond.)* **220**, 569–592.
- Delaney, M.F., Woodward, A.R., Kiltie, R.A. & Moore, C.T. (2011). Mortality of American alligators attributed to cannibalism. *Herpetologica* **67**, 174–185.
- DeVault, T.L. & Rhodes, O.E., Jr (2002). Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. *Acta Theriol.* **47**, 185–192.
- Diefenbach, C.O.C. (1975a). Gastric function in *Caiman crocodylus* (Crocodylia: Reptilia). I. Rate of gastric digestion and gastric motility as a function of temperature. *Comp. Biochem. Physiol.* **51A**, 259–265.
- Diefenbach, C.O.C. (1975b). Gastric function in *Caiman crocodylus* (Crocodylia: Reptilia). II. Effects of temperature on pH and proteolysis. *Comp. Biochem. Physiol.* **51A**, 267–274.
- Diefenbach, C.O.C. (1979). Ampullarid gastropod – staple food of *Caiman latirostris*? *Copeia* **1979**, 162–163.
- Diefenbach, C.O.C. (1981). Regurgitation is normal in Crocodylia. *Cienc. Cult.* **33**, 82–83.
- Dowler, B. (1846). *Contributions to the natural history of the alligator (Crocodylus mississippiensis with a microscopic addendum*. New Orleans: B.M. Norman Publishers.
- Eaton, M. & Barr, B. (2005). Africa. Republic of Congo. *IUCN Croc. Spec. Group Newsl.* **24**, 18–20.
- Ehrlich, P.R., Dobkin, D.S. & Wheye, D. (1988). *The birders handbook: a field guide to the natural history of North American birds*. New York: Simon and Schuster.
- Elias, T.S. (1987). *The complete trees of North America: field guide and natural history*. New York: Gramercy Publishing Company.
- Engel, T.R. (1997). Seed dispersal and plant regeneration by snakes? *Ecotropica* **3**, 33–41.
- Fialho, R.F. (1990). Seed dispersal by a lizard and a tree frog – effect of dispersal site on seed survivorship. *Biotropica* **22**, 423–424.
- Fisher, D.C. (1981). Crocodylian scatology, microinvertebrate concentrations, and enamel-less teeth. *Paleobiology* **7**, 262–275.

- Fitch-Snyder, H. & Lance, V.A. (1993). Behavioral observations of lithography in captive juvenile alligators. *J. Herpetol.* **27**, 335–357.
- Ford, D.K. & Moll, D. (2004). Sexual and seasonal variation in foraging patterns in the stinkpot, *Sternotherus odoratus*, in southwestern Missouri. *J. Herpetol.* **38**, 296–301.
- Forkner, B. (Ed.) (1996). *John James Audubon: selected journals and other writings*. New York: Penguin Books.
- Foster, W.C. (1998). *The La Salle expedition to Texas: the journal of Henri Joutel, 1684–1687*. Austin: Texas State Historical Association.
- Fukuda, Y., Webb, G., Manolis, C., Delaney, R., Letnic, M. & Lindner, G. (2011). Recovery of saltwater crocodiles following unregulated hunting in tidal rivers of the Northern Territory, Australia. *J. Wildl. Mgmt.* **75**, 1253–1266.
- Galdikas, B.M.F. & Yeager, C.P. (1984). Crocodile predation on a crab-eating macaque in Borneo. *Am. J. Primatol.* **6**, 49–51.
- Gans, C. (1989). Crocodylians in perspective! *Am. Zool.* **29**, 1051–1054.
- Garnett, S.T. (1985). The consequences of slow chitin digestion on crocodylian diet analysis. *J. Herpetol.* **19**, 303–304.
- Godfrey, R.K. & Wooten, J.W. (1979). *Aquatic and wetland plants of southeastern United States*. Athens: University of Georgia Press.
- Graham, S.P. & Sorrell, G.G. (2008). *Kinosternon subrubrum* (Eastern mud turtle). Diet. *Herpetol. Rev.* **39**, 218.
- Guppy, H. (1917). *Plants, seeds, and currents in the West Indies and Azores*. London: Williams and Norgate.
- Hartley, L.M., Glor, R.E., Sproston, A.L., Powell, R. & Parmelee, J.S., Jr (2000). Germination rates of seeds consumed by two species of rock iguanas (*Cyclura* spp.) in the Dominican Republic. *Caribb. J. Sci.* **36**, 149–152.
- Hartley, W. & Hartley, E. (1977). *The alligator: king of the wilderness*. New York: Thomas Nelson, Inc.
- Hawthorne, W.D. & Parren, M.P.E. (2000). How important are forest elephants to the survival of woody plant species in Upper Guinea forests? *J. Trop. Ecol.* **16**, 133–150.
- Herrera, C.M. (1985). Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos* **44**, 132–141.
- Herrera, C.M. (1988). Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. *Oikos* **55**, 250–262.
- Herrera, C.M. (2002). Seed dispersal by vertebrates. In *Plant-animal interactions: an evolutionary approach*: 185–208. Herrera, C.M. & Pellmyr, O. (Eds). Oxford: Oxford University Press.
- Horna, J.V., Cintra, R. & Ruesta, P.V. (2001). Feeding ecology of black caiman *Melanosuchus niger* in a western Amazonian forest: the effects of ontogeny and seasonality on diet composition. *Ecotropica* **7**, 1–11.
- Howe, H.F. (1985). Gomphothere fruits: a critique. *Am. Nat.* **125**, 853–865.
- Howe, H.F. & Miriti, M.N. (2004). When seed dispersal matters. *Bioscience* **54**, 651–660.
- Howe, H.F. & Smallwood, J. (1982). Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* **13**, 201–228.
- Hutton, J. (1989). Movements, home range, dispersal and the separation of size classes in Nile crocodiles. *Am. Zool.* **29**, 1033–1049.
- Irvine, F.R. (1953). Herbivorous snakes. *Br. J. Herpetol.* **1**, 173.
- Iverson, J.B. (1979). Behavior and ecology of the rock iguana *Cyclura carinata*. *Bull. Fla. State Mus. Biol. Sci.* **24**, 175–358.
- Janes, D. & Gutzke, W.H.N. (2002). Factors affecting retention time of turtle scutes in stomachs of American alligators, *Alligator mississippiensis*. *Am. Midl. Nat.* **148**, 115–119.
- Janzen, D.H. (1981). Digestive seed predation by a Costa Rican Baird's tapir. *Biotropica* **13**, 150–156.
- Janzen, D.H. (1982). Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents. *Oikos* **38**, 150–156.
- Janzen, D.H. (1984). Dispersal of small seeds by big herbivores: foliage is the fruit. *Am. Nat.* **123**, 338–353.
- Joanen, T. & McNease, L. (1972). A telemetric study of adult male alligators on Rockefeller Refuge, Louisiana. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* **26**, 252–275.
- Jordano, P. (1992). Fruits and frugivory. In *Seeds: the ecology of regeneration in plant communities*: 105–156. Fenner, M. (Ed.). Wallingford: Commonwealth Agricultural Bureau International.
- Kay, W.R. (2004). Movements and home ranges of radio-tracked *Crocodylus porosus* in the Cambridge Gulf region of Western Australia. *Wildl. Res.* **31**, 495–508.
- Kellogg, R. (1929). *The habits and economic importance of alligators*. Tech. Bull. No. 147. Washington, DC: US Department of Agriculture.
- Kimmons, J.B. & Moll, D. (2010). Seed dispersal by red-eared sliders (*Trachemys scripta elegans*) and common snapping turtles (*Chelydra serpentina*). *Chelonian Conserv. Biol.* **9**, 289–294.
- Kofron, C.P. (1993). Behavior of Nile crocodiles in a seasonal river in Zimbabwe. *Copeia* **1993**, 463–469.
- Kunkel, G. (1965). *The trees of Liberia: field notes on the more important trees of Liberian forests, and a field identification key*. Report No. 3 of German Forestry Mission to Liberia. München Basel Wien: Bayerischer Landwirtschaftsverlag.
- Lambert, J.E. & Garber, P.A. (1998). Evolutionary and ecological implications of primate seed dispersal. *Am. J. Primatol.* **45**, 9–28.
- Lance, V.A., Elsey, R.M., Trosclair, P.L., III & Nunez, L. (2011). Long-distance movement by American alligators in southwest Louisiana. *Southeast. Nat.* **10**, 389–398.
- Lang, J.W. (1987). Crocodylian behaviour: implications for management. In *Wildlife management: crocodiles and alliga-*

- tors: 273–294. Webb, G.J.W., Manolis, S.C. & Whitehead, P.J. (Eds). Sydney: Surrey Beatty and Sons Pty., Ltd.
- Lazell, J.D. & Spitzer, N.C. (1977). Apparent play behavior in an American alligator. *Copeia* **1977**, 188.
- Leighton, M. & Leighton, D.R. (1983). Vertebrate response to fruiting seasonality within a Bornean rain forest. In *Tropical rain forest ecology and management*: 181–196. Sutton, S.L., Whitmore, T.C. & Chadwick, A.C. (Eds). Oxford: Blackwell Scientific Publications.
- Liu, H., Platt, S.G. & Borg, C.K. (2004). Seed dispersal by the Florida box turtle (*Terrapene carolina bauri*) in pine rockland forests of the lower Florida Keys, United States. *Oecologia* **138**, 539–546.
- Magnusson, W.E., da Silva, E.V. & Lima, A.P. (1987). Diets of Amazonian crocodylians. *J. Herpetol.* **21**, 85–95.
- McIlhenny, E.A. (1935). *The alligator's life history*. Boston: Christopher Publishing House.
- McNease, L. & Joanen, T. (1977). Alligator diets in relation to marsh salinity. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies* **31**, 36–40.
- McWilliams, S.R., Afik, D. & Secor, S. (1997). Patterns and processes in the vertebrate digestive system. *Trends Ecol. Evol.* **12**, 420–422.
- Moll, D. & Jansen, K.P. (1995). Evidence for a role in seed dispersal by two tropical herbivorous turtles. *Biotropica* **27**, 121–127.
- Mookerjee, S. (1946). Mango fruit – on the menu of the common python (*Python molurus*). *J. Bombay Nat. Hist. Soc.* **46**, 733.
- Morelet, A.M. (1871). *Travels in Central America including accounts of some regions unexplored since the conquest*. New York: Leypoldt, Holt, and Williams.
- Mors, W.B. & Rizzini, C.T. (1966). *Useful plants of Brazil*. San Francisco: Holden-Day Publishers.
- Murray, K.G., Russell, S., Picone, C.M., Winnett-Murray, K., Sherwood, W. & Kuhlmann, M.L. (1994). Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology* **75**, 989–994.
- Neill, W.T. (1971). *The last of the ruling reptiles: alligators, crocodiles, and their kin*. New York: Columbia University Press.
- Nogales, M., Delgado, J.D. & Medina, F.M. (1998). Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). *J. Ecol.* **86**, 866–871.
- Nogales, M., Quilis, V., Medina, F.M., Mora, J.L. & Trigo, L.S. (2002). Are predatory birds effective secondary seed dispersers? *Biol. J. Linn. Soc.* **75**, 345–352.
- Pauwels, O.S.G., Barr, B., Sanchez, M.L. & Burger, M. (2007). Diet records for the dwarf crocodile, *Osteolaemus tetraspis tetraspis* in Rabi Oil Fields and Loango National Park, southwestern Gabon. *Hamadryad* **31**, 258–264.
- Peaker, M. (1969). Active acquisition of stomach stones in a specimen of *Alligator mississippiensis* Daudin. *Br. J. Herpetol.* **4**, 103–104.
- Peres, C.A. (2000). Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conserv. Biol.* **14**, 240–253.
- van der Pijl, L. (1982). *Principles of dispersal in higher plants*. New York: Springer.
- Platt, S.G., Brantley, C.G. & Hastings, R.W. (1990). Food habits of juvenile American alligators in the upper Lake Pontchartrain estuary. *Northeast Gulf Sci.* **11**, 23–130.
- Platt, S.G. & Elsey, R.M. (2011). Possible consumption of corn by American alligators at wildlife feeders in Louisiana, USA. *IUCN Croc. Spec. Group Newsl.* **30**, 27–28.
- 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. *Herpetol. J.* **16**, 281–290.
- Platt, S.G., Rainwater, T.R. & McMurry, S.T. (2002). Diet, gastrolith acquisition and initiation of feeding among hatchling Morelet's crocodiles in Belize. *Herpetol. J.* **12**, 81–84.
- 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. *Southwest. Nat.* **52**, 310–317.
- Platt, S.G., Rainwater, T.R., Thorbjarnarson, J.B., Finger, A.G., Anderson, T.A. & McMurry, S.T. (2009). Size estimation, morphometrics, sex ratio, sexual size dimorphism, and biomass of Morelet's crocodile in northern Belize. *Caribb. J. Sci.* **45**, 1–14.
- Platt, S.G., Rainwater, T.R., Thorbjarnarson, J.B. & Martin, D. (2011). Size estimation, morphometrics, sex ratio, sexual size dimorphism, and biomass of *Crocodylus acutus* in the coastal zone of Belize. *Salamandra* **47**, 179–192.
- 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. *Herpetol. Nat. Hist.* **9**, 183–188.
- 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. *J. Herpetol.* **47**, 1–10.
- Pooley, A.C. (1989). Food and feeding habits. In *Crocodyles and alligators*: 76–91. Ross, C.A. & Garnett, S. (Eds). New York: Facts on File.
- Radford, A.E. & Bell, C.R. (1968). *Manual of the vascular flora of the Carolinas*. Chapel Hill: University of North Carolina Press.
- Read, M.A. & Anderson, A.J. (2000). Proteolytic and starch-digesting enzymes of the stomach, duodenum and pancreas of post-hatchling estuarine crocodiles *Crocodylus porosus*. In *Crocodylian biology and evolution*: 317–326. Grigg, G.C., Seebacher, F. & Franklin, C.E. (Eds). Sydney: Surrey Beatty and Sons Pty. Ltd.

- Rice, A.N. (2004). *Diet and condition of American alligators (Alligator mississippiensis) in three central Florida lakes*. MSc thesis, University of Florida, Gainesville, Florida, USA.
- Richardson, B.A., Brunsfeld, S.J. & Klopfenstein, N.B. (2002a). DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). *Mol. Ecol.* **11**, 215–227.
- Richardson, K.C., Webb, G.J.W. & Manolis, S.C. (2002b). *Crocodyles: inside and out*. Sydney: Surrey Beatty & Sons, Pty. Ltd.
- Ridley, H.N. (1930). *The dispersal of plants through the world*. Ashford: L. Reeve and Co., Ltd.
- Rootes, W.L. & Chabreck, R.H. (1993). Reproductive status and movement of adult female alligators. *J. Herpetol.* **27**, 121–126.
- Rosenblatt, A.E. & Heithaus, M.R. (2011). Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *J. Anim. Ecol.* **80**, 786–798.
- Russo, S.E. & Augspurger, C.K. (2004). Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecol. Lett.* **7**, 1058–1067.
- Saalfield, D.T. (2010). *American alligator (Alligator mississippiensis) ecology in inland wetlands of East Texas*. MSc thesis, Stephen F. Austin State University, Nacogdoches, Texas, USA.
- Sáez, F. & Traveset, A. (1995). Fruit and nectar feeding by *Podarcis lilfordi* (Lacertidae) on Cabrera archipelago (Balearic Islands). *Herpetol. Rev.* **26**, 121–123.
- Schmidt, K.P. (1924). Notes on Central American crocodyles. *Fieldiana* **12**, 79–92.
- Schupp, E.W. (1993). Quantity, quality, and the effectiveness of seed dispersal by animals. In *Frugivory and seed dispersal: ecological and evolutionary aspects*: 15–30. Fleming, T.H. & Estrada, A. (Eds). Boston: Kluwer Academic Publishers.
- Schupp, E.W., Howe, H.F., Augspurger, C.K. & Levey, D.J. (1989). Arrival and survival in tropical treefall gaps. *Ecology* **70**, 562–564.
- Schupp, E.W., Jordano, P. & Gómez, J.M. (2010). Seed dispersal effectiveness revisited: a conceptual review. *New Phytol.* **188**, 333–353.
- Scott, T.P. & Weldon, J.P. (1990). Chemoreception in the feeding behaviour of adult American alligators, *Alligator mississippiensis*. *Anim. Behav.* **39**, 398–405.
- Shoop, C.R. & Ruckdeschel, C.A. (1990). Alligators as predators on terrestrial mammals. *Am. Midl. Nat.* **124**, 407–412.
- Smith, G.A. & Coulson, R.A. (1992). Nutrition of *Crocodylus niloticus*. In *Conservation and utilization of the Nile crocodile in southern Africa: handbook on crocodile farming*: 79–105. Smith, G.A. & Marias, J. (Eds). Johannesburg: Crocodylian Study Group of Southern Africa.
- Soares, D. (2002). An ancient sensory organ in crocodylians. *Nature* **417**, 241–242.
- Sokol, O. (1971). Lithography and geophagy in reptiles. *J. Herpetol.* **5**, 67–71.
- Standley, P.C. (1961). *Trees and shrubs of Mexico. Volume 23*. Washington, DC: United States National Herbarium, Smithsonian Institution.
- Staton, M.A. (1988). *Studies on the use of fats and carbohydrates in the diet of American alligators (Alligator mississippiensis)*. PhD dissertation, University of Georgia, Athens, Georgia, USA.
- Staton, M.A. & Dixon, J.R. (1975). Studies on the dry season biology of *Caiman crocodilus crocodilus* from the Venezuelan llanos. *Memoria de la Sociedad de Ciencias Naturales La Salle* **35**, 237–266.
- Staton, M.A., Edwards, H.M., Jr, Brisbin, I.L., Jr, McNease, L. & Joanen, T. (1990). Protein and energy relationships in the diet of the American alligator (*Alligator mississippiensis*). *J. Nutr.* **120**, 775–785.
- Stone, M.D. & Moll, D. (2009). Abundance and diversity of seeds in digestive tracts of *Terrapene carolina* and *T. ornata* in southwestern Missouri. *Southwest. Nat.* **54**, 346–350.
- Taylor, J.A., Webb, G.J.W. & Magnusson, W.E. (1978). Methods of obtaining stomach contents from live crocodyles. *J. Herpetol.* **12**, 415–417.
- Thorbjarnarson, J. (1992). *Crocodyles: an action plan for their conservation*. Gland: IUCN Publications.
- Thorbjarnarson, J.B. (1993a). Diet of the spectacled caiman (*Caiman crocodilus*) in the central Venezuelan llanos. *Herpetologica* **49**, 108–117.
- Thorbjarnarson, J.B. (1993b). Fishing behavior of the spectacled caiman in the Venezuelan llanos. *Copeia* **1993**, 1166–1171.
- Tiffney, B.H. (1986). Evolution of seed dispersal syndromes according to the fossil record. In *Seed dispersal*: 273–305. Murray, D.R. (Ed.). San Diego: Academic Press.
- Tovée, M.J. (1995). Ultra-violet photoreceptors in the animal kingdom: their distribution and function. *Trends Ecol. Evol.* **10**, 455–460.
- Traveset, A. (1990). *Ctenosaura similis* Gray (Iguanidae) as a seed disperser in a Central American deciduous forest. *Am. Midl. Nat.* **123**, 402–404.
- Traveset, A. (1998). Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspect. Plant Ecol. Evol. Syst.* **1**, 151–190.
- Tucker, A.D., Limpus, C.J., McCallum, H.I. & McDonald, K.R. (1997). Movements and home ranges of *Crocodylus johnstoni* in the Lynd River, Queensland. *Wildl. Res.* **24**, 379–396.
- Tucker, A.D., McCallum, H.I., Limpus, C.J. & McDonald, K.R. (1998). Sex-biased dispersal in a long-lived polygynous reptile (*Crocodylus johnstoni*). *Behav. Ecol. Sociobiol.* **44**, 85–90.

- Valentine, J.M., Walther, J.R., McCartney, K.M. & Ivy, L.M. (1972). Alligator diets on the Sabine National Wildlife Refuge, Louisiana. *J. Wildl. Mgmt.* **36**, 809–815.
- Valido, A. & Nogales, M. (1994). Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* **70**, 403–411.
- Valido, A., Nogales, M. & Medina, F.M. (2003). Fleshy fruits in the diet of Canarian lizards *Gallotia galloti* (Lacertidae) in a xeric habitat of the island of Tenerife. *J. Herpetol.* **37**, 741–747.
- Vanzolini, P.E. & Gomes, N. (1979). Notes on the ecology and growth of Amazonian caimans (Crocodylia, Alligatoridae). *Papéis Avulsos de Zoologica* **32**, 205–216.
- Varela, R.O. & Bucher, E.H. (2002). Seed dispersal by *Chelonoidis chilensis* in the Chaco dry woodland of Argentina. *J. Herpetol.* **36**, 137–140.
- Vosburgh, J.R. (1949). *Texas lion hunter*. San Antonio: The Naylor Company.
- Wallace, K.M. & Leslie, A.J. (2008). Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *J. Herpetol.* **42**, 361–368.
- Webb, G.J.W. & Manolis, C. (1989). *Crocodyles of Australia*. Frenchs Forest: Reed Books Pty., Ltd.
- Weldon, P.J., Swenson, D.J., Olson, J.K. & Brinkmeier, W.G. (1990). The American alligator detects food chemicals in aquatic and terrestrial environments. *Ethology* **85**, 191–198.
- Wheelwright, N.T. & Orians, G.H. (1982). Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *Am. Nat.* **119**, 402–413.
- Whitaker, A.M. (1987). The role of lizards in New Zealand plant reproductive strategies. *N. Z. J. Bot.* **25**, 315–328.
- Whitaker, R. & Whitaker, Z. (1984). Reproductive biology of the mugger (*Crocodylus palustris*). *J. Bombay Nat. Hist. Soc.* **81**, 297–316.
- Willson, M.F. (1993). Mammals as seed dispersal mutualists in North America. *Oikos* **67**, 159–176.
- Zeveloff, S.I. (2002). *Raccoons: a natural history*. Washington, DC: Smithsonian Institution Press.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Studies reporting vegetation in crocodylian diets. Size class: Y = yearling; J = juveniles; SA = subadults; A = adults. NR = not reported. Asterisk denotes studies based on fecal analyses.