Niche partitioning between juvenile sympatric crocodilians in Mesangat Lake, East Kalimantan, Indonesia

Agata Staniewicz[1*], Natascha Behler[2,3], Soeimah Dharmasyah[4], Gareth Jones[1]

Abstract. Crocodilians are apex predators and sympatric species are likely to have different ecologies or morphologies in order to minimise competition between species, i.e., niche partitioning. Here, we examined the ecological niche factors that may affect competition between juvenile Siamese crocodiles (*Crocodylus siamensis*) and Tomistoma (*Tomistoma schlegelii*) in Mesangat Lake — the only documented area where the two species co-exist. This location has also been subjected to recent disturbance from logging and oil palm development. We identified and compared preferred habitats and stomach contents of each species. *Tomistoma schlegelii* were found predominantly in flooded forests, while *C. siamensis* were mainly in open areas. However, overlap in prey choice between juvenile *T. schlegelii* and *C. siamensis* was significantly higher than expected by chance and invertebrates were the most frequent prey items in both species. High overlap in prey choice between the two species suggests that juvenile *T. schlegelii* and *C. siamensis* are generalist predators. Furthermore, the evidence of separation of habitat combined with overlap in prey choice indicates competition-driven niche partitioning between *C. siamensis* and *T. schlegelii*. This paper provides basis for co-ordinated conservation efforts for the two threatened species in this unique ecosystem.

Key words. Crocodiles, tropical wetlands, diet, Sunda gharial, Borneo

INTRODUCTION

According to Hutchinson (1957), an ecological niche is the total range of conditions under which an organism or population lives and replaces itself. Niches can be considered overlapping when two individuals use the same resources, and if these resources are in short supply, niche overlap can cause competition and lead to niche shifts for one or both organisms, or competitive exclusion of one of them (Pianka, 1994; Ouboter, 1996). In natural situations niches often overlap where two species coexist, yet as the niche is dynamic in space and time and comprised of several dimensions (Pianka, 1994; Ouboter, 1996), competition is reduced. Niche shifts dividing habitat (MacArthur & Wilson, 1967), food or temporal activity (Root, 1967; Ouboter, 1996) can also help reduce competition between coexisting species.

Apex predators such as crocodilians have a top-down effect on the regulation of ecosystem structure (Nifong & Silliman, 2013) and the disappearance of the predator can lead to cascading changes in community dynamics (Estes et al., 2011). While predator avoidance can still affect young crocodiles, habitat, food, nesting season and location as well as time of activity are the ecological factors most likely to be affected by competition (Ouboter, 1996).

Globally, the distribution of crocodilians spans all tropical and subtropical regions, yet there are relatively few areas where any of the extant 24 species coexist (Herron, 1994; Ouboter, 1996; Ross, 2001; Shirley et al., 2014). Ouboter (1996) identified 31 pairs of sympatric crocodilians, mostly involving one geographically wide ranging species overlapping with a species with a narrower range, e.g., *Crocodylus niloticus* and *Mecistops cataphractus* (Shirley et al., 2015), *Crocodylus porosus* and *Tomistoma schlegelii* (Shaney et al., 2017). Such range overlap does not mean the species are syntopic; many sympatric crocodilians occupy different habitats (Ouboter, 1996).

The Siamese crocodile (*Crocodylus siamensis*) and Tomistoma (*Tomistoma schlegelii*) — which are considered critically endangered and vulnerable on the IUCN Red List of Threatened Species (Bezuijen et al., 2014) — historically occurred across continental and insular Southeast Asia (Stuebing et al., 2006). Present ranges are fragmented and have reduced in size, but both species inhabit Kalimantan (Indonesian Borneo) (Cox et al., 1993). *Crocodylus siamensis* is mainly found in isolated lakes and swamps of Cambodia (Platt et al., 2006b) but has recently been rediscovered in East Kalimantan in the Mahakam River basin, where it occurs in marshes and open lakes with floating vegetation mats (Cox et al., 1993; Ross et al., 1998). *Tomistoma schlegelii*

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appears to be broadly distributed in lowland river systems of Borneo and Sumatra, and inhabits peat swamp forests and adjacent wetlands, preferring sluggish freshwater tributaries and lakes (Ross et al., 1998; Bezuijen et al., 2001; Auliya et al., 2006; Stuebing et al., 2006). Although the ranges of the two species overlap in Kalimantan, different habitat preferences were proposed that lead to habitat partitioning, with *T. schlegelii* occupying lakes, streams and rivers and *C. siamensis* preferring more stagnant overgrown swamps and lakes (Ross et al., 1998). However, both species coexist in Mesangat Lake, a wetland northeast of Mahakam River basin comprising patches of degraded secondary forest and areas of open water covered with floating vegetation.

Sympatric crocodilian species usually have different snout shapes (Ouboter, 1996; Brochu, 2001; Pearcy, 2011). In Mesangat Lake, the longirostrine *T. schlegelii* is found together with the brevirostrine *C. siamensis* (Fig. 1). Snout shape is related to feeding (Busbey, 1995) and prey choice (Ouboter, 1996). Long narrow snouts and sharp teeth of longirostrine species enable quick movements underwater and are thought to be specialised for the capture of agile slippery prey, such as fishes (Whitaker & Basu, 1982). Brevirostrine species have broader snouts, which can increase drag and hence reduce speed under water, but allow the animals to take a variety of prey, including larger reptiles, birds and mammals.

While few published studies on *C. siamensis* diet are available, examination of faecal samples in Cambodia and Lao People's Democratic Republic (PDR) (Daltry, 2003; Simpson & Han, 2004; Bezuijen, 2010) suggests that *C. siamensis* is a generalist feeder similar to other brevirostrine *Crocodylus* species. *Tomistoma schlegelii* was initially thought to feed primarily on fishes (Neill, 1971), yet based on local interviews and examination of stomach contents from a few captured individuals, Bezuijen et al. (1997) reported that *T. schlegelii* in Sumatra has a much broader diet. Anecdotal reports of *T. schlegelii* preying on primates (Galdikas & Yeager, 1984; Galdikas, 1985; Yeager, 1991) also suggest that the species may be an opportunistic and generalist feeder. However, the diet of juvenile *T. schlegelii* in the wild is largely unknown, and based on the stomach contents of three individuals captured in Sumatra, their diet consisted mainly of small aquatic invertebrates and fishes (Bezuijen et al., 2001).

Nesting preferences of the two species appear to be different. In Cambodia and Lao PDR, *C. siamensis* build mound nests both on land and on floating vegetation mats during the late dry season (Bezuijen et al., 2006; Platt et al., 2006b). In East Kalimantan, *C. siamensis* nests have been found on floating vegetation mats in the late dry and early rainy seasons (Ross et al., 1998). Very few *T. schlegelii* nests have been documented in the wild (Bezuijen et al., 1997, 2001, 2002, 2005; Ross et al., 1998) and among these the majority are described as dry vegetation mounds (about 2 m in diameter and 0.5 m high) built in the early dry season at a base of a tree near the water line.
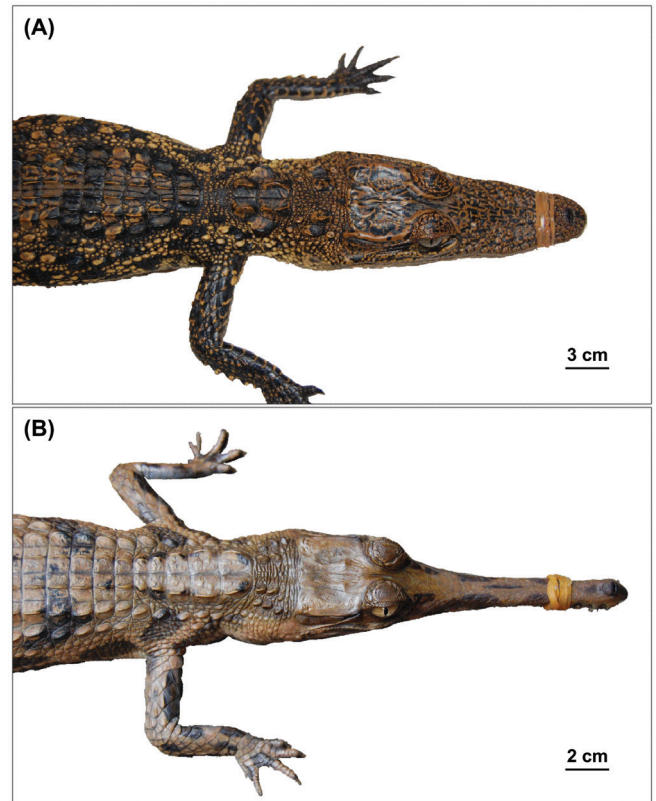

Fig. 1. Wild juvenile *Crocodylus siamensis* (A) and *Tomistoma schlegelii* (B) captured in Mesangat Lake.

In this study, we investigated coexistence patterns of *T. schlegelii* and *C. siamensis* in Mesangat Lake. For this approach we examined four ecological niche factors — habitat, diet, nesting habitat and season — that may affect competition between the species. As niche overlap leads to competition, we hypothesise niche partitioning to occur in one or more of these factors as a means of minimising competition. Additionally, we attempt to determine if juvenile *T. schlegelii* are specialist or generalist feeders.

MATERIAL & METHODS

Study site. The Lower Mahakam River area in East Kalimantan contains several large seasonal lakes, and hundreds of smaller ones, forming a wetland exceeding half a million hectares (MacKinnon et al., 1996; Chokkalingam et al., 2005). This includes Mesangat Lake (00°31′06″N, 116°41′47″E), a wetland extending over approximately 18,500 hectares between the Kelinjau and Telen rivers (Stuebing et al., 2015), and flooded during the rainy season, fed by several small river backflows and inflows.

The area has been heavily logged since the 1970s and some of the forests around Mesangat were burnt during the forest fires in 1982–83 and 1997–98 (Chokkalingam et al., 2005). Most of the open areas are covered in floating grass mats of *Leeria hexandra*, *Thoracostachyum sumatranum* and *Scleria* spp. sedges (Kurniati et al., 2005). Additionally, exotic floating plant species (water hyacinth, *Eichhornia crassipes*; water fern, *Salvinia cucullata*) cover large parts of both forested and open areas of Mesangat.

The dry season lasts from June to October, and the rainy season from November to May. Overall daily mean temperature during the field seasons was 27.3°C, with mean high of 33.8°C and a mean low of 23.5°C. The daily mean water temperature was 27.8°C. The water level in Mesangat varies throughout the year both within and between the seasons, ranging from 31–381 cm. The floating vegetation limits boat access to many areas, and this is further restricted during the dry season when the water level drops and dry patches of grass vegetation mats appear.

Fish are harvested from Mesangat on a daily basis using gillnets, fish hooks, bamboo traps and electrofishing (Hadiaty, 2009), and the numbers of fishermen active in the area have been increasing, from approximately 15 in 1996 to 50 in 2005 (Kurniati et al., 2005).

Crocodile surveys and capture. To identify crocodile habitats and nesting seasons we conducted surveys in rainy, dry and transitional rainy-to-dry seasons. We carried out a total of 107 spotlight surveys by boat between 2000–0200 hours, over three field seasons: rainy (October–December 2010, 26 surveys, water level range: 103–333 cm), dry (June–September 2011, 44 surveys, water level range: 30–110 cm) and transitional (May–June 2012, 37 surveys, water level range: 100–340 cm).

When a crocodile was spotted, the animal was approached and when possible captured either by hand, scoop net or with a snare pole. We took standard morphometric measurements (Simpson, 2006) of the animals caught and marked them with tail scute clips (Bolton, 1989). Additionally, we tagged each *T. schlegelii* with an external bead tag placed on the right posterior side of the nuchal rosette for easy identification.

If the crocodile escaped, we identified it to species if possible, and recorded the unidentified individuals as eye shine only (EO). At each point of sighting we logged the GPS coordinates and identified the type of vegetation if present. We estimated body length of the observed animal and allocated it to one of five body length group categories: hatchlings (0–50 cm), small juveniles (51–100 cm), large juveniles (101–150 cm), subadults (151–200 cm) and adults (>200 cm).

Habitat preferences. To assess the available habitat we surveyed 10 transect lines at different locations classified either as either open areas (10.9 km total), or flooded forests (5.6 km total) during the transitional season. Transects were limited to routes accessible by boat and thus excluded grass mats and thick floating vegetation. Using a Shotsaver S400 laser range finder (accuracy 1 m), we measured the distance to the nearest tree and the nearest floating grass mat at 100 m intervals at the transect line (165 points total). Where visible, we also measured the distance to the nearest exotic floating plants (Fig. 2). In 2012, we recorded the same parameters at each point of crocodile sighting or capture to determine the preferred habitat for each species.
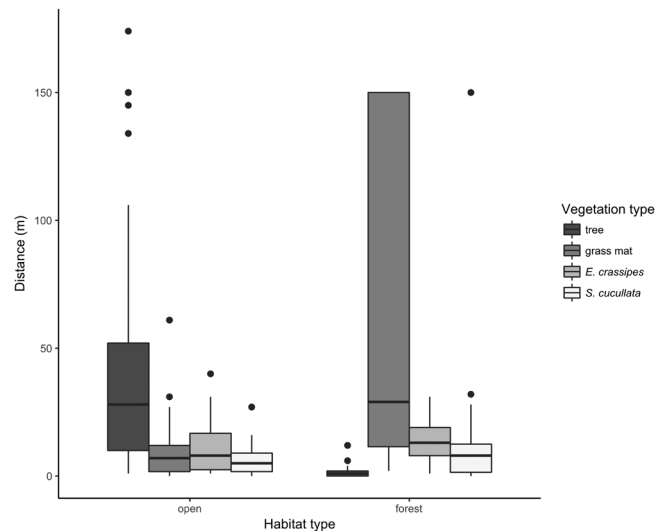

Fig. 2. Boxplots of the distance to the nearest tree, floating grass mat, and invasive floating plants *Eicchornia crassipes* and *Salvinia cucullata* in the two main habitat types in Mesangat wetland: the open areas and the flooded forest. The habitats differ significantly in median distance from a transect line point to the nearest tree (W = 5807.5, n_{open} = 109, n_{forest} = 56, P < 0.001). Floating grass mats are present predominantly in the open areas where median distance from the transect to the nearest grass mat was significantly smaller than in flooded forest (W = 697, n_{open} = 108, n_{forest} = 39, P < 0.001). The invasive plant species, *E. crassipes* and *S. cucullata*, were found in both habitats. Median distances from transect points to the nearest exotic plant did not differ significantly between the flooded forest and open areas (*E. crassipes*: W = 186.5, n_{open} = 22, n_{forest} = 24, P = 0.089; *S. cucullata*: W = 801, n_{open} = 48, n_{forest} = 39, P = 0.249).

Diet preferences. Immediately after capture we removed stomach contents from 26 *T. schlegelii* (total body length [TTL] ± standard deviation = 71.4 ± 19.6 cm) and four *C. siamensis* (TTL ± SD = 108.6 ± 34 cm) following a modified flushing technique (Taylor et al., 1978; Platt et al., 2006a). The crocodiles sustained no apparent injuries from this process. Stomach contents were preserved in 5% formalin solution. We identified the intact food item parts to the lowest taxonomic level possible using a dissection microscope. Further, we supplemented the data for analysis with information on the stomach contents from 12 *C. siamensis* captured in 2010–2011 provided by Behler et al. (2018).

Statistical analysis. All statistical analyses were carried out in R 3.3.3 (R Core Team, 2017) using a significance level of 0.05. To identify habitat preferences, we compared the median distances of sightings of the two species to the four nearest vegetation types from 10 habitat transects using Mann-Whitney tests. To determine habitat preferences of *T. schlegelii* and *C. siamensis* we performed Mann-Whitney tests comparing the median distances to the nearest floating grass mat and the nearest tree from the point of crocodile sighting and/or capture in the 2012 field season.

To calculate prey choice overlap between juvenile *T. schlegelii* and *C. siamensis* in Mesangat Lake we used Pianka's index for niche overlap (Pianka, 1973). We used EcoSimR 1.0 (Gotelli et al., 2015) to create 1,000 random
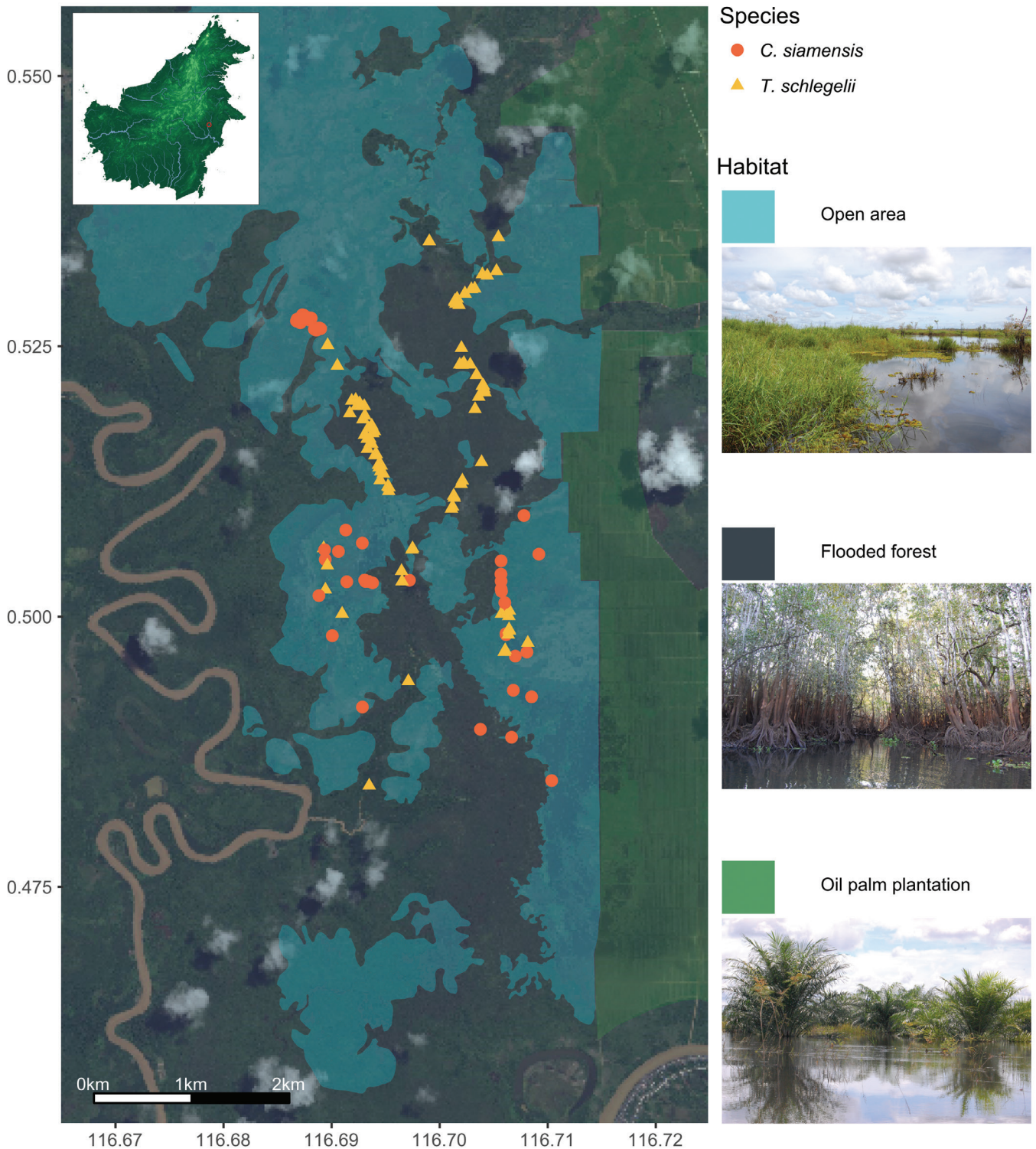
Fig.3. Locations of *C. siamensis* and *T. schlegelii* spotted in Mesangat Lake habitats in the three seasons: wet (2010), dry (2011) and transitional (2012). Data on *C. siamensis* distribution in 2010 and 2011 refer to Behler et al. (2018). Base map: ArcMap Bing Aerial.

matrices using Randomisation Algorithm 3 for the two species with six prey item categories and compared the observed and randomly generated levels of prey choice overlap to determine whether prey overlap is greater or less than expected by chance (Razgour et al., 2011). Crocodilians show ontogenetic shifts in diet (Delany & Abercrombie, 1986). To account for possible differences between animals of different sizes, we calculated prey choice overlap between the smaller (50–90 cm TTL) and larger (>90 cm TTL) animals.

RESULTS

Crocodile distribution and habitat preferences. Both *C. siamensis* and *T. schlegelii* were recorded in Mesangat Lake in all three seasons. The total numbers of sightings of animals identified either to species or as EO varied between seasons, from 155 crocodiles spotted in the rainy season, 91 in the transitional to 58 encountered during the dry season (Table 1).

Table 1. Total numbers of crocodile sightings in Mesangat Lake during each field season with animals identified either to species or as eye shine only (EO). Numbers of animals successfully captured and marked after spotting, and additional crocodiles captured by the fishermen (*) throughout the field season. Data on *C. siamensis* sighted and captured in 2010–2011 from Behler et al. (2018).

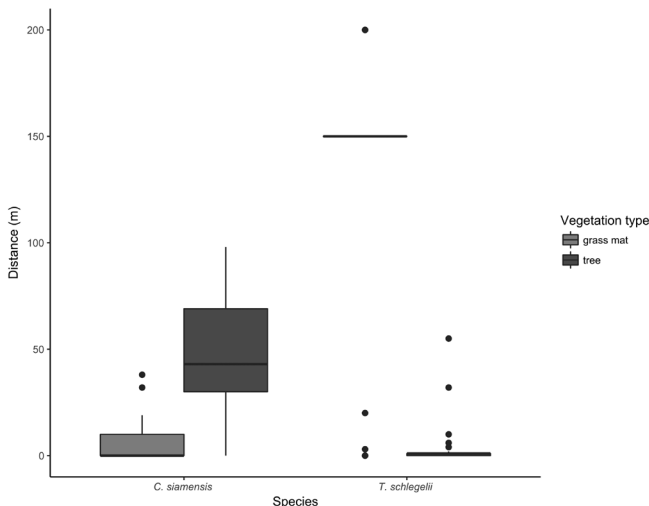| Field season	Crocodiles observed				Crocodiles captured		
	C. siamensis	*T. schlegelii*	EO	Total	*C. siamensis*	*T. schlegelii*	Total
2010 (wet)	30	58	67	155	6*	4	10
2011 (dry)	5	45	8	58	4*	13 (+7*)	24
2012 (transitional)	38	29	24	91	10 (+4*)	6	20

Fig. 4. Boxplots of the distance to the nearest tree and the nearest floating grass mat of *T. schlegelii* (n = 28) and *C. siamensis* (n = 33) spotted and/or captured in Mesangat wetland in May–June 2012. All *C. siamensis* and 7% of *T. schlegelii* sightings occurred in open areas with floating grass mats. *Tomistoma schlegelii* was found at significantly larger median distances from grass mats than *C. siamensis* (W = 823, n_1 = 28, n_2 = 33, P < 0.001) and significantly closer to the nearest tree (W = 129.5, n_1 = 28, n_2 = 33, P < 0.001).

Throughout the study period crocodiles were encountered in flooded forests and open areas (Fig. 3). Of crocodile sightings identified to species, 84% of *T. schlegelii* and 2% of *C. siamensis* were found in locations classified as forested. The remaining 98% of *C. siamensis* and 16% *T. schlegelii* were recorded in open areas with floating vegetation (Fig. 4). *Tomistoma schlegelii* was found in rivers with seasonally flooded land banks as well as in permanently flooded wetland areas. *Crocodylus siamensis* was only sighted in the flooded open wetland.

We examined three nests found by local fishermen during the study, one found in 2011, belonging to *T. schlegelii*, and two *C. siamensis* nests recorded in 2012. Two of the nests had an adult crocodile present (*T. schlegelii* and *C. siamensis* respectively) either during the visit or captured on camera trap footage. The remaining nest was covered with egg shells and at night 10 hatchlings of *C. siamensis* were seen swimming in 30 m distance from the nest in open water at the edge of a grass mat. The *T. schlegelii* nest was a mound composed of dried leaves and vegetation, built on land at the base of a tree, 4 m from the water line. The

C. siamensis nests were floating dried vegetation mounds attached to floating grass mats in open areas.

Crocodile sizes. All crocodiles caught during the study were hatchlings and juveniles (31–137.5 cm TTL). Thirty *T. schlegelii* (TTL ± SD = 75 ± 19.1 cm) were captured and marked in the three field seasons. Additionally, four juvenile *C. siamensis* (TTL ± SD = 108.6 ± 34 cm) and 10 hatchlings (TTL ± SD = 32.6 ± 1.7 cm) were captured in May–June 2012. Three marked *T. schlegelii* were recaptured within the seasons: one in 2010 and two in 2011. None of the marked *T. schlegelii* were recaptured between the seasons.

Throughout the three field seasons 172 crocodile sightings identified to species were classified into five estimated size classes (Fig. 5). The majority of sightings were allocated to 51–100 cm TTL (54% *C. siamensis* and 61% *T. schlegelii*) and 0–50 cm TTL (25% *C. siamensis* and 29% *T. schlegelii*). Larger juveniles (101–150 cm TTL; 10% *C. siamensis* and 8% *T. schlegelii*), subadults (151–200 cm TTL; 4% *C. siamensis* and 0% *T. schlegelii*) and adults (>200 cm TTL; 7% *C. siamensis* and 2% *T. schlegelii*) were encountered less frequently.

The number of hatchlings (0–50 cm TTL) encountered varied significantly between the field seasons (χ^2 = 22.03, df = 2, P < 0.001). In October–December 2010 small *T. schlegelii* of this size class were spotted more frequently, while in May–June 2012, more *C. siamensis* of the same size class were encountered. The frequency of encounter of small juveniles (51–100 cm TTL) did not differ significantly between seasons (χ^2 = 4.72, df = 2, P = 0.094).

Diet preferences. Juveniles of both species consumed a diverse array of invertebrates and vertebrates, as well as plant material (Fig. 6). Invertebrates, including insects, arachnids and crustaceans were the most frequent prey, and were identified in stomach content samples of all *T. schlegelii* and 87.5% of *C. siamensis*. Amongst vertebrates, fishes were the most common prey in both species (in 68.6% of *C. siamensis* and 38.4% of *T. schlegelii* samples). Mammal hair was found in 56.3% of *C. siamensis* but only 7.7% *T. schlegelii*. Frogs, reptiles and birds were poorly represented in the diet of both species. Non-food items recovered included flowers, grass, pieces of wood and vegetation found in stomach of 62.5% of *C. siamensis* and 42.3% of *T. schlegelii* (Table 2).
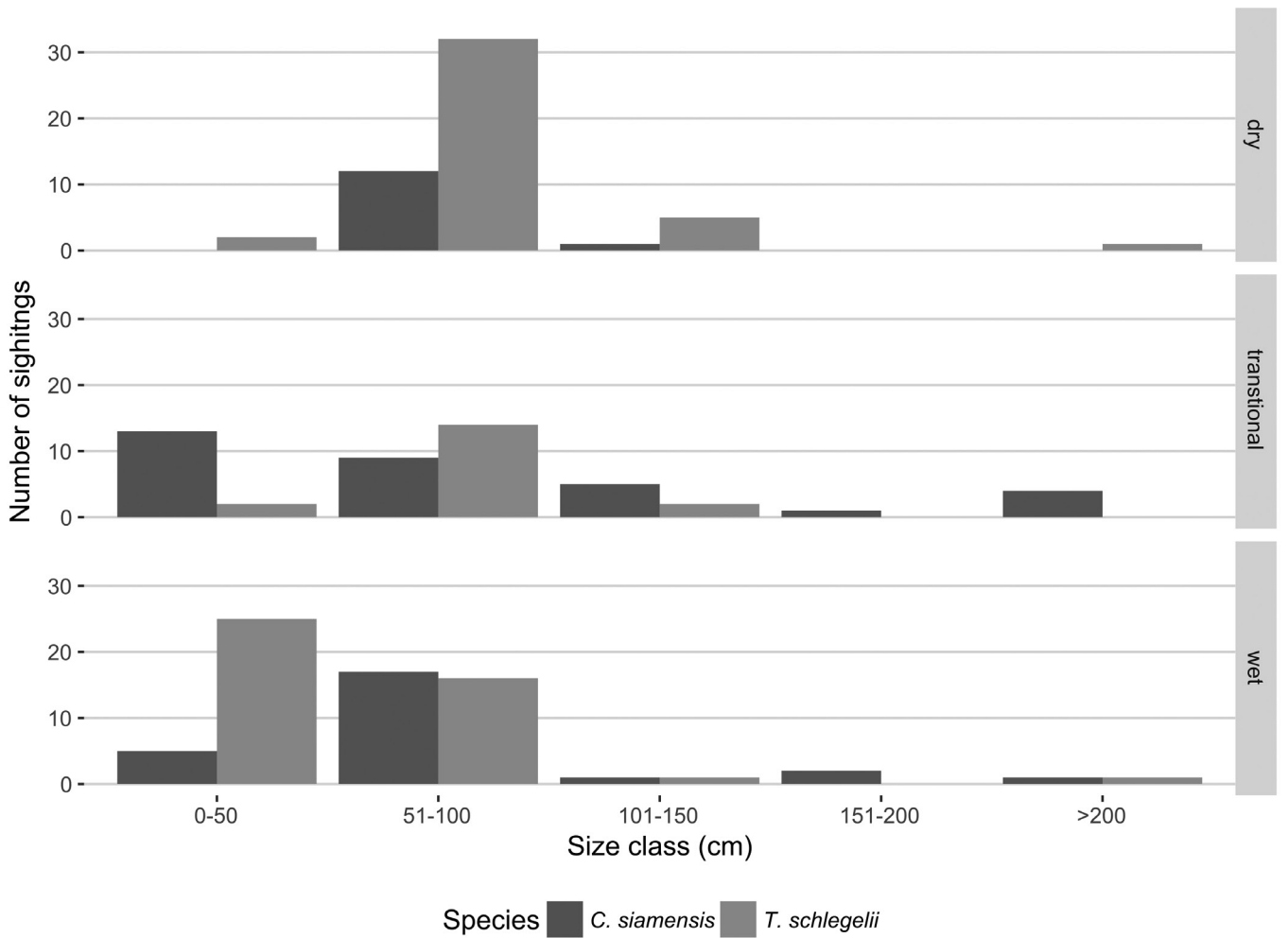
Fig. 5. Sightings of *C. siamensis* (n = 71) and *T. schlegelii* (n = 101) belonging to different estimated size classes, spotted in Mesangat Lake during different seasons: dry (2011), transitional (2012) and wet (2010).
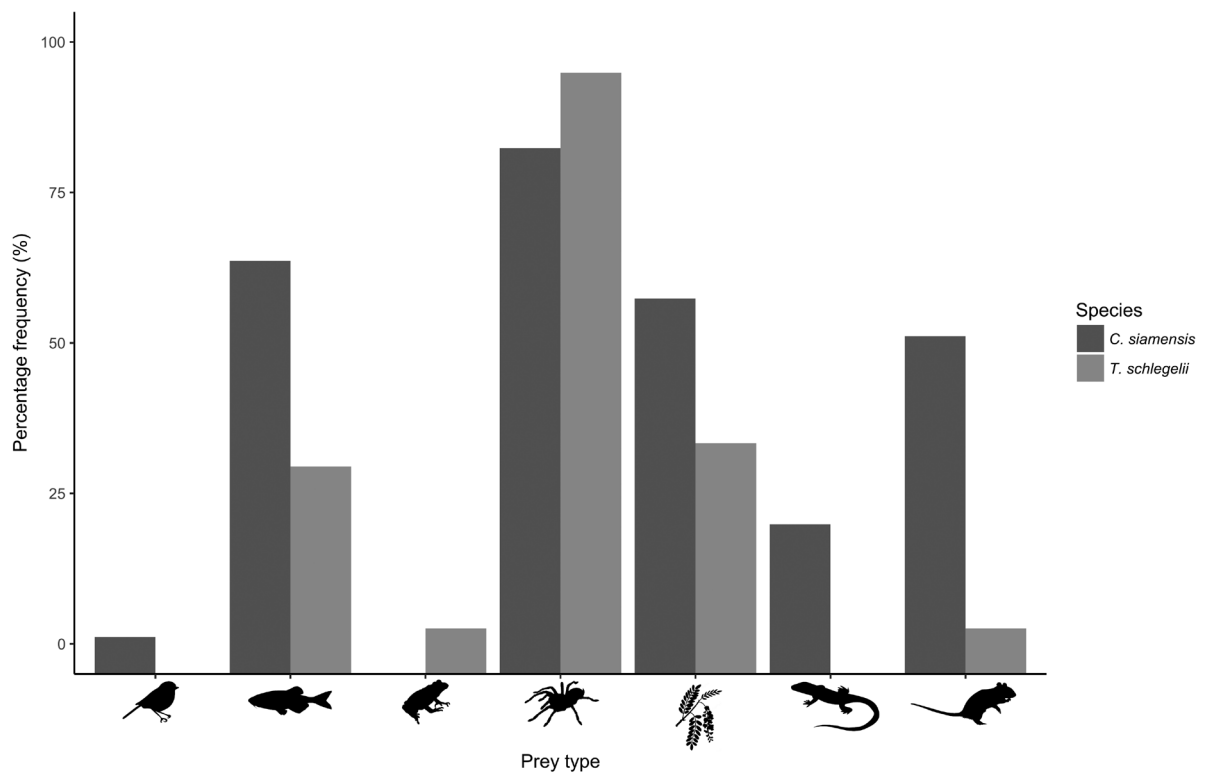

Fig. 6. Percentage of stomach content samples of *C. siamensis* (n = 16) and *T. schlegelii* (n = 26) containing different prey items: birds, fish, amphibians, invertebrates, plants, reptiles and mammals.

Table 2. Prey and non-food items identified to the lowest taxonomic level found in stomach contents of *Tomistoma schlegelii* (n = 26) and *Crocodylus siamensis* (n = 16*) captured in Mesangat Lake over 2010–2012 field seasons. Number of crocodiles containing each prey item followed by percent occurrence (%) of stomachs with given prey item types within the total of each species.

Category	Taxon	Crocodile species	
		T. schlegelii	*C. siamensis*
Invertebrates	Arachnids	7 (26.9)	–
	Coleoptera (water beetles)	8 (30.8)	1 (6.3)
	Lepidoptera (butterflies and moths)	4 (15.4)	–
	Odonata (adult dragonflies)	4 (15.4)	–
	Orthoptera (grasshoppers and crickets)	4 (15.4)	1 (6.3)
	Diptera (flies)	4 (15.4)	–
	Hymenoptera (ants)	4 (15.4)	–
	Freshwater shrimp	1 (3.8)	–
	Unidentified invertebrates	20 (76.9)	14 (87.5)
Fishes	Unidentified fishes	10 (38.4)	11 (68.8)
Frogs	*Hylarana erythrea*	2 (7.7)	0
Reptiles	Unidentified reptiles	0	4 (25)
Birds	Unidentified birds	0	1 (6.3)
Mammals	Unidentified mammals	2 (7.7)	9 (56.3)
Plant matter	Grass	6 (23.1)	1 (6.3)
	Flowers	5 (19.2)	–
	Wood	3 (11.5)	–
	Unidentified vegetation	0	9 (56.3)

– Data not available, classified as "unidentified invertebrates" or "unidentified vegetation"; *12 *C. siamensis* from (Behler et al., 2018).

Insects, crustaceans and arachnids were grouped together as invertebrates for analysis, with fishes, frogs, reptiles, birds and mammals as the remaining prey categories. Prey choice overlap (O_{jk} = 0.85) between 26 juvenile *T. schlegelii* (TTL ± SD = 71.4 ± 19.6 cm) and 16 juvenile *C. siamensis* (TTL ± SD = 93 ± 21.8 cm) was significantly higher than expected by chance (P[Observed>Expected] = 0.015).

Ontogenetic differences in prey choice between small (<90 cm TTL) and large (>90 cm TTL) juvenile crocodiles were not detected and prey choice overlap could not be distinguished from a random distribution of prey type in relation to crocodile size class both within *C. siamensis* (n_{small} = 9, n_{large} = 7, O_{jk} = 0.95, P[Observed=Expected] = 0.01), *T. schlegelii* (n_{small} = 20, n_{large} = 6, O_{jk} = 0.95, P[Observed=Expected] = 0.04), and between species (n_{small} = 28, n_{large} = 13, O_{jk} = 0.94, P[Observed=Expected] = 0.001).

DISCUSSION

The two freshwater crocodile species in Mesangat Lake favour different habitats. *Tomistoma schlegelii* was found predominantly in flooded forest and at close distance to nearby trees, away from floating grass mats. *Crocodylus siamensis* was mainly recorded in open areas near floating vegetation, at a clear distance from trees. These results are in accordance with earlier reports on habitat use by *T. schlegelii* and *C. siamensis* in other areas within their ranges (Ross et al., 1998; Bezuijen et al., 2001).

The majority of animals seen in Mesangat Lake were juveniles. Young crocodilians may have different environmental requirements from adults, e.g., salinity, food or shelter (Ouboter, 1996), or avoid conflict with adults (Hutton, 1989; Somaweera et al., 2013). Our data are not sufficient to determine whether the low frequency of sightings of adult crocodiles is a result of habitat partitioning between different size groups (Auliya et al., 2006), juvenile to adult mortality, or if larger animals are warier of people (Ron et al., 1998).

The main limitation of spotlight surveys is that they only allow detection of crocodiles present on the surface. Thus they can be less effective with highly aquatic species that spend a lot of time underwater. Differences in habitat and vegetation structure can conceal crocodiles and introduce further bias (Ouboter, 1996). While the spotlight surveys in Mesangat enabled detection of *T. schlegelii* and *C. siamensis* in different habitats, indices for population density and abundance could not be provided. The low recapture rate of marked *T. schlegelii* individuals is likely to result from increased wariness (Ron et al., 1998) as well as high mortality rates of hatchling and juvenile crocodilians (Webb et al., 1983; Hussain, 1999). Although syntopic crocodile species are expected to occur in lower densities as a result of competition (Ouboter, 1996), ecological studies on abundance and population density in both crocodilians are pending.

Tomistoma schlegelii and *C. siamensis* appear to nest in different habitats and in different seasons, yet the small

sample sizes do not allow definitive conclusions. Both *C. siamensis* nests were vegetation mounds on floating grass mats similar to other nests attributed to the species found in the area (Ross et al., 1998). The characteristics of the *T. schlegelii* nest, a mound built on land at a base of a tree, is also consistent with previous reports for the species (Bezuijen et al., 1997, 2001, 2002, 2005; Ross et al., 1998). Although Ross (1998) reported one *T. schlegelii* nest on a floating grass mat in the open area in Mesangat Lake, it is possible that this nest belonged to *C. siamensis*. The nesting habitats are consistent with the species' preferred habitats in Mesangat Lake, even though *C. siamensis* in Lao PDR have been reported nesting on land as well as on floating vegetation (Bezuijen et al., 2006).

The nests and hatchlings of *C. siamensis* and *T. schlegelii* were found in different seasons, suggesting possible nesting season partitioning between species. Since *T. schlegelii* nests are built on land and incubation lasts 72–90 days (Trutnau & Sommerlad, 2006), the dry season may trigger nesting behaviour when water levels are low. The nest discovered in August 2011 is consistent with the nesting season reported by Ross (1998), falling between July and October. Both *C. siamensis* nests were found in May 2012 during the transitional season. The presence of hatchlings indicates the end of nesting season. However, earlier reports identify August–September as the start of *C. siamensis* nesting season in Mesangat Lake (Ross et al., 1998) and nests belonging to the species have been found there throughout the year (Rob Stuebing, pers. comm.). Yet, as climate change affects the onset of dry and rainy seasons, influencing crocodile behaviour (Bickford et al., 2010), the timing of future breeding seasons is likely to be less predictable. *Tomistoma schlegelii* and *C. siamensis* both build mounds in the area. Vegetation mounds are typical for species nesting in the rainy season on floating grass mats that adapt to changing water levels, therefore the possibility of flooding is reduced (Ouboter & Nanhoe, 1987). Mound nests built during the dry season are at a higher risk of temperature variations and are usually built under trees to prevent desiccation (Ouboter & Nanhoe, 1987; Ouboter, 1996). In sympatric crocodilians that both build mounds, a shift to nesting in dry season can occur in one of the species to avoid competition with the other (Ouboter & Nanhoe, 1987). As *T. schlegelii* appears to also nest in the dry season in areas where *C. siamensis* is absent (Bezuijen et al., 2002, 2005), competition avoidance may justify the observed different timing of nesting behaviour in *C. siamensis* in Mesangat Lake.

Overlap in diet could induce interspecific competition and result in habitat partitioning. MacArthur & Wilson (1967) suggested that sympatric species will rather shift habitat niche than diet, to avoid competition. Juvenile *T. schlegelii* and *C. siamensis* in Mesangat Lake feed on a variety of invertebrates and small vertebrates. High overlap in prey may indicate both species are generalist feeders. However, similar diets are observed in juveniles of many crocodilian species, both in longirostrine *C. johnstoni* (Webb et al., 1982; Tucker et al., 1996) and brevirostrine *Alligator mississippiensis* (Delany, 1990), *Caiman crocodilus* (Thorbjarnarson, 1993),

Crocodylus moreletii (Platt et al., 2006a) and *Crocodylus porosus* (Taylor, 1979). All crocodilians are opportunistic ambush predators and will eat invertebrates and small vertebrates as juveniles, shifting to larger prey as they grow in size (Delany & Abercrombie, 1986; Platt et al., 2006a; Borteiro et al., 2009). Although *C. siamensis* captured in Mesangat Lake were larger and preyed on more mammals and fishes than *T. schlegelii*, diet overlap between larger and smaller crocodiles could not be distinguished from random overlap in diet expected to occur by chance, possibly due to the small sample size. Determining whether potential differences in diet are due to ontogenetic prey shift or differences in prey preference, possibly related to snout morphology, requires further analysis of larger specimens from both species. Vegetation devoured by both species is likely to be a result of accidental ingestion while hunting on the water surface. While some crocodile species have been found eating a variety of plants including fruits (Platt et al., 2013), grass and small flowers found in the stomach contents of *C. siamensis* and *T. schlegelii* correspond to the floating vegetation on the surface of Mesangat Lake, the habitat of many invertebrate prey species. High overlap in prey choice between the species presented here suggests that juvenile *T. schlegelii* and *C. siamensis* are generalist predators. Furthermore, the evidence of separation of habitat, combined with overlap in prey choice, may indicate competition-driven niche partitioning between *C. siamensis* and *T. schlegelii*.

Crocodiles in Mesangat Lake inhabit both open wetland and the remaining patches of swamp forest. The patchy habitat is an important fishing site for the local communities, and the only documented site where *C. siamensis* and *T. schlegelii* occur sympatrically. Furthermore, Mesangat Lake is considered an important crocodile conservation area that harbours Indonesia's only breeding population of *C. siamensis*. Sympatric crocodilians influence each other's ecology (Webb et al., 1983; Pearcy, 2011), thus conservation efforts for *C. siamensis* and *T. schlegelii* in Mesangat Lake should be well co-ordinated. In 2016, both Mesangat Lake and the neighbouring Kenohan Suwi wetlands have been proposed as Essential Ecosystem Areas (EEAs), a scheme providing protection for the endangered species which occur outside of national parks, while still allowing some sustainable use of resources (Platt, 2018). Further monitoring of the effects of human activities such as fishing and palm oil development on the crocodile populations will be essential for conservation planning (Stuebing et al., 2015). Together, the freshwater crocodiles could act as flagship and umbrella species for large-scale wetland habitat conservation initiatives.

and WAZA. The use of animals has been approved by the University of Bristol Ethical Review Group (UIN number: UB/10/032) and RISTEK (Permit numbers: 0162/SIP/FRP/SM/VI/2011 and 116/SIP/FRP/SM/V/2012).

LITERATURE CITED

Auliya M, Shwedick BM, Sommerlad R, Brend S & Samedi (2006) A short-term assessment of the conservation status of *Tomistoma schlegelii* (Crocodylia: Crocodylidae) in Tanjung Puting National Park (Central Kalimantan, Indonesia)., 36 pp.

Behler N, Kopsieker L, Staniewicz A, Darmansyah S, Stuebing R & Ziegler T (2018) Population size, demography and feeding preferences of the Siamese crocodile *Crocodylus siamensis* (Schneider, 1801) in the Mesangat Swamp in Kalimantan, Indonesia. Raffles Bulletin of Zoology, 66: 506–516.

Bezuijen M (2010) *Crocodylus siamensis diet*. Herpetological Review, 41: 10–11.

Bezuijen M, Hartoyo P, Elliott M & Baker B (1997) Project Tomistoma: second report on the ecology of the false gharial (*Tomistoma schlegelii*) in Sumatra. Sanderson, Northern Territory, Australia.

Bezuijen M, Hasudungan F, Kadarisman R, Webb G, Wardoyo S, Manolis S & Samedi (2002) False gharial (*Tomistoma schlegelii*) surveys in southeast Sumatra, Indonesia (1995-2002). Darwin, Australia, 30 pp.

Bezuijen M, Phothitay C, Hedemark M & Chanrya S (2006) Preliminary status review of the Siamese crocodile (*Crocodylus siamensis* Schneider, 1801) (Reptilia: Crocodylia) in the Lao People's Democratic Republic. Vientiane, Lao PDR.

Bezuijen M, Shwedick B, Simpson B, Staniewicz A & Stuebing R (2014) *Tomistoma schlegelii*. The IUCN Red List of Threatened Species. http://www.iucnredlist.org/details/21981/0. (Accessed 10 10 2017)

Bezuijen M, Suryansyah B, Huda I, Pratjihno P, Andriyono S, Potess L & Sommerlad R (2005) False gharial (*Tomistoma schlegelii*) surveys in West Kalimantan, Indonesia in 2004. Frankfurt and Pontianak.

Bezuijen M, Webb G, Hartoyo P & Samedi (2001) Peat swamp forest and the false gharial *Tomistoma schlegelii* (Crocodilia, Reptilia) in the Merang River, eastern Sumatra, Indonesia. Oryx, 35: 301–307.

Bickford D, Howard SD, Ng DJJ & Sheridan JA (2010) Impacts of climate change on the amphibians and reptiles of Southeast Asia. Biodiversity and Conservation, 19: 1043–1062.

Bolton M (1989) The management of crocodiles in captivity. FAO Conservation Guide 22, Rome, Italy.

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.

Brochu C (2001) Crocodylian snouts in space and time: phylogenetic approaches toward adaptive radiation. American Zoologist, 41: 564–585.

Busbey A (1995) The structural consequences of skull flattening in crocodilians. In: J. J. Thomason (ed.), Functional Morphology in Vertebrate Paleontology. Cambridge University Press, Cambridge, pp. 173–192.

Chokkalingam U, Kurniawan I & Ruchiat Y (2005) Fire, livelihoods, and environmental change in the Middle Mahakam peatlands, East Kalimantan. Ecology and Society, 10: 26.

Cox J, Frazier R & Maturbongs R (1993) Freshwater crocodiles of Kalimantan (Indonesian Borneo). Copeia, 1993: 564–566.

Daltry J (2003) Status of the Siamese crocodile in the Central and Southern Cardamom Mountains, Cambodia: Findings of recent 'Kropeu Phnom' surveys. Fauna & Flora International, Cambodia Programme: Phnom Penh, 62 pp.

Delany M (1990) Late summer diet of juvenile American alligators. Journal of Herpetology, 24: 418–421.

Delany M & Abercrombie C (1986) American alligator food habits in northcentral Florida. The Journal of Wildlife Management, 50: 348–353.

Estes J, Terborgh J, Brashares J, Power M, Berger J, Bond W, Carpenter S, Essington T, Holt R, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R & Wardle DA (2011) Trophic downgrading of planet Earth. Science, 333: 301–306.

Galdikas B (1985) Crocodile predation on a proboscis monkey in Borneo. Primates, 26: 495–496.

Galdikas B & Yeager C (1984) Crocodile predation on a crab-eating macaque in Borneo. American Journal of Primatology, 6: 49–51.

Gotelli N, Hart E & Ellison A (2015) EcoSimR: Null model analysis for ecological data. https://cran.r-project.org/web/packages/EcoSimR/EcoSimR.pdf. (Accessed 15 July 2017).

Hadiaty R (2009) The freshwater fish diversity around Mesangat watershed, District Muara Ancalong, Regency Kutai Kartanegara, Province Kalimantan Timur. Cibinong.

Herron J (1994) Body size, spatial distribution, and microhabitat use in the caimans, *Melanosuchus niger* and *Caiman crocodilus*, in a Peruvian Lake. Journal of Herpetology, 28: 508–513.

Hussain S (1999) Reproductive success, hatchling survival and rate of increase of gharial *Gavialis gangeticus* in National Chambal Sanctuary, India. Biological Conservation, 87: 261–268.

Hutchinson G (1957) Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22: 415–427.

Hutton J (1989) Movements, home range, dispersal and the separation of size classes in Nile crocodiles. American Zoologist, 29: 1033–1049.

Kurniati H, Widodo T & Manolis S (2005) Surveys of Siamese crocodile (*Crocodylus siamensis*) habitat in the Mahakam River, East Kalimantan, Indonesia. Cibinong.

MacArthur R & Wilson E (1967) The Theory of Island Biogeography. Princeton University Press, Princeton.

MacKinnon K, Hatta I, Halim H & Mangalik A (1996) The Ecology of Kalimantan. Periplus Editions (HK) Ltd, Singapore, 802 pp.

Neill W (1971) The Last of the Ruling Reptiles. Alligators, Crocodiles, and Their Kin. Columbia University Press, New York, 486 pp.

Nifong J & Silliman B (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.

Ouboter P (1996) Ecological studies on crocodilians in Suriname: niche segregation and competition in three predators. SPB Academic Publishing, Amsterdam, 139 pp.

Ouboter P & Nanhoe L (1987) Notes on nesting and parental care in *Caiman crocodilus crocodilus* in northern Suriname and an analysis of crocodilian nesting habitats. Amphibia-Reptilia, 8: 331–348.

Pearcy A (2011) Implications of skull shape for the ecology and conservation biology of crocodiles. Leiden University.

Pianka E (1973) The structure of lizard communities. Annual Review of Ecology and Systematics, 4: 53–74.

Pianka E (1994) Evolutionary Ecology. 5th Edition. HarperCollins College Publishers, New York.

Platt S (2018) Securing the last wild Siamese crocodile population in Indonesia: preliminary results of surveys at Lake Mesangat. Crocodile Specialist Group Newsletter, 37: 7–12.

Platt S, Elsey R, Liu H, Rainwater T, Nifong J, Rosenblatt A, Heithaus M & Mazzotti F (2013) Frugivory and seed dispersal

by crocodilians: an overlooked form of saurochory? Journal of Zoology.

Platt S, Rainwater T, Finger A, Thorbjarnarson J, Anderson T & McMurry S (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, Sovannara H, Kheng L, Stuart B & Walston J (2006b) *Crocodylus siamensis* along the Sre Ambel River, southern Cambodia: habitat, nesting, and conservation. Herpetological Natural History, 9: 183–188.

R Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. (Accessed 15 July 2017).

Razgour O, Korine C & Saltz D (2011) Does interspecific competition drive patterns of habitat use in desert bat communities? Oecologia, 167: 493–502.

Ron S, Vallejo A & Asanza E (1998) Human influence on the wariness of *Melanosuchus niger* and *Caiman crocodilus* in Cuyabeno, Ecuador. Journal of Herpetology, 32: 320–324.

Root R (1967) The niche exploitation pattern of the blue-gray gnatcatcher. Ecological Monographs, 37: 317–350.

Ross C, Cox J, Kurniati H & Frazier S (1998) Preliminary surveys of palustrine crocodiles in Kalimantan. In: Crocodiles: Proceedings of the 14th Working Meeting of the the IUCN-SSC Crocodile Specialist Group. Singapore.

Ross J (1998) Crocodiles: status survey and conservation action plan. 2nd Edition. IUCN/SSC Crocodile Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK, viii + 96 p.

Ross J (2001) Why are there so few species of crocodilians? In: G. C. Grigg, F. Seebacher, & C. E. Franklin (eds.), Crocodilian Biology and Evolution. Surrey Beatty and Sons, Chipping Norton, pp. 1–2.

Shaney KJ, Hamidy A, Walsh M, Arida E, Arimbi A & Smith EN (2017) Impacts of anthropogenic pressures on the contemporary biogeography of threatened crocodilians in Indonesia. Oryx, (May): 1–12.

Shirley MH, Villanova VL, Vliet KA & Austin JD (2015) Genetic barcoding facilitates captive and wild management of three cryptic African crocodile species complexes. Animal Conservation, 18: 322–330.

Shirley MH, Vliet KA, Carr AN & Austin JD (2014) Rigorous approaches to species delimitation have significant implications for African crocodilian systematics and conservation. Proceedings of The Royal Society B, 281: 20132483.

Simpson B (2006) Siamese Crocodile Survey and Monitoring Handbook Siamese Crocodile Survey and Monitoring Handbook. Fauna and Flora International, Phnom Penh, Cambodia, 79 pp.

Simpson B & Han S (2004) Siamese crocodile (*Crocodylus siamensis*) surveys in Cambodia. In: Crocodiles: Proceedings of the 17th Working Meeting of the IUCN-SSC Crocodile Specialist Group. Darwin, Australia, Volume 1945.

Somaweera R, Brien M & Shine R (2013) The Role of Predation in Shaping Crocodilian Natural History. Herpetological Monographs, 27: 23–51.

Stuebing R, Bezuijen M, Auliya M & Voris H (2006) The current and historic distribution of *Tomistoma schlegelii* (the False gharial) (Muller, 1838) (Crocodylia, Reptilia). The Raffles Bulletin of Zoology, 54: 181–197.

Stuebing R, Sommerlad R & Staniewicz A (2015) Conservation of the Sunda gharial *Tomistoma schlegelii* in Lake Mesangat, Indonesia. International Zoo Yearbook, 49: 137–149.

Taylor JA (1979) The foods and feeding habits of subadult *Crocodylus porosus* Schneider in Northern Australia. Australian Wildlife Research, 6: 347–359.

Taylor J, Webb G & Magnusson W (1978) Methods of obtaining stomach contents from live crocodilians (Reptilia, Crocodilidae). Journal of Herpetology, 12: 415–417.

Thorbjarnarson J (1993) Diet of the spectacled caiman (*Caiman crocodilus*) in the Central Venezuelan Llanos. Herpetologica, 49: 108–117.

Trutnau L & Sommerlad R (2006) Crocodilians. Their Natural History & Captive Husbandry. Chimaira, Frankfurt am Main, Germany, 646 pp.

Tucker A, Limpus C, McCallum H & McDonald K (1996) Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. Copeia, 1996: 978–988.

Webb G, Buckworth R & Manolis S (1983) *Crocodylus johnstoni* in the McKinlay River, N.T. VI.* Nesting biology. Australian Wildlife Research, 10: 607–637.

Webb G, Manolis S & 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, Manolis S & Sack G (1983) *Crocodylus johnstoni* and *C. porosus* coexisting in a tidal river. Australian Wildlife Research, 10: 639–650.

Whitaker R & Basu D (1982) The gharial (*Gavialis gangeticus*) - A review. Journal of Bombay Natural History Society, 79: 531–548.

Yeager C (1991) Possible antipredator behavior associated with river crossings by proboscis monkeys (*Nasalis larvatus*). American Journal of Primatology, 24: 61–66.