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Population size, demography and diet of the Siamese crocodile, *Crocodylus siamensis* (Schneider, 1801) in the Mesangat Swamp in Kalimantan, Indonesia

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Abstract. A study of the distribution, abundance and diet of the critically endangered Siamese crocodile (*Crocodylus siamensis*) was undertaken during 2010 and 2011 in the Mesangat wetland, East Kalimantan, Indonesia. It provides the first hard data concerning the ecology of the species outside of mainland Indochina. Crocodiles were captured if possible, weighed, measured and tagged subcutaneously with a Passive Integrated Transponder (PIT tag). Forty-three (43) non-hatchling *C. siamensis* were identified, of which seven were adults. An estimate of total non-hatchling population size was calculated from individuals marked in 2010 and re-captured in 2011, extrapolated to the area of all locations where *C. siamensis* were seen. The total population size in the survey area was estimated to be approximately 75 individuals. Ninety-one percent (91%) of all *C. siamensis* detections (n=77) occurred outside the forest-type habitat, adjacent to or within two meters of floating grassy mats. The first investigation on stomach contents of the species was undertaken in this study. Diet samples from 13 *C. siamensis* were obtained from stomach lavage and analysed individually. Prey found in stomach contents contained insect remnants, snail shells, fish bones, bird feathers, snake scales and small mammal fur and varied considerably between individuals. The presence of necrophagic ants suggested that *C. siamensis* consume carrion. The current study confirmed at least one healthy breeding population of *C. siamensis* outside of the mainland of Indochina and provides important data for the species' long-term conservation in Kalimantan.

Key words. crocodiles, Kalimantan, Mesangat, *siamensis*, *Tomistoma*

INTRODUCTION

The Siamese crocodile, *Crocodylus siamensis* (Schneider, 1801), is one of the most threatened crocodilians in the world. The species has been listed as critically endangered on the Red List of Threatened Species by IUCN since 1996 (Bezuijen et al., 2012) and is included on Appendix I of CITES. Available records indicate that *C. siamensis* occurs in slow-flowing rivers, swamps and marshes (Bezuijen et al., 2012). It is a medium-sized crocodilian with males reaching up to 4 m in length (Smith, 1919). Information on the ecology and behaviour of the species remains limited (Bezuijen et al., 2012).

C. siamensis is native to Indonesia and its historical distribution encompassed Thailand, Vietnam, Laos, Cambodia, Malaysia and possibly Myanmar (Ross, 1986; Platt & Lee, 2000; Cox & Phothitay, 2008). The current distribution is greatly fragmented and the total population has decreased by more than 80% compared to its historical abundance (Ross et al., 1998), mainly due to threats from hunting, capture for crocodile farming (Simpson & Sam, 2004; Kurniati et al., 2005), egg collection, habitat loss (Trutnau & Sommerlad, 2005) and incidental capture in fishing gear (Bezuijen et al., 2012).

Reintroduction and reinforcement programmes have been implemented in Vietnam, where the species was nearly extirpated, as well as in Thailand (Polet et al., 2002; Temsiripong et al., 2004) and Cambodia (Daltry & Starr, 2010; Sam et al., 2015; Eam et al., 2017). In Indonesia, it was thought that *C. siamensis* had gone extinct, until Cox et al. (1993), Cox (2004) and Kurniati et al. (2005) indicated the species exists in at least one remaining site: Danau (Lake) Mesangat, also called Mesangat wetland or swamp. Danau Mesangat is a lowland wetland of about 120 km^2 (Stuebing et al., 2015), which is located within the East Kalimantan province on the island of Borneo (Fig. 1). It is surrounded

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Fig. 1. The Mesangat wetland in East Kalimantan (inset: the Mesangat position within Kalimantan). Black – Villages; Black with Red dot – Survey locations; maps modified after © OpenStreetMap).

by 12 villages within the sub-district of Muara Ancalong. In Danau Mesangat, *C. siamensis* shares its habitat with the Sunda gharial, *Tomistoma schlegelii* (Müller, 1838) which is distinguishable from *C. siamensis* by its chocolate brown coloration and its long, narrow snout.

Further investigation is required to evaluate the status of *C. siamensis* in Danau Mesangat and through a systematic scientific assessment contribute to the long-term conservation of the species. This paper presents the results of the first in-depth study of the only known wild population of *C. siamensis* outside of mainland Southeast Asia. The study describes the distribution of *C. siamensis* in Danau Mesangat, approximates the population size and demography, and for the first time investigates the species' diet by analysing the stomach contents of captured, and subsequently released, individuals.

MATERIAL AND METHODS

Field site. Danau Mesangat (0°30′07″ N, 116°41′54″ E) belongs to the Mahakam river system. It is a permanently flooded former peat swamp habitat at an elevation of 20 m above sea level located approximately 150 km inland from the coast. The Mesangat wetland is located between two rivers, the Kelinjau and the Telen, joining at their junction downstream to form the Kedang Kepala, which flows into the Mahakam (Fig. 1). Substantial areas of the wetland are covered in permanently submerged forests, in which the water level varies between a depth of 30 and 380 cm during seasonal flooding. In open areas, the water surface is covered almost entirely with floating vegetation, namely *Eichhornia crassipes, Salvinia cucullata* (both invasive species), *Hanguana malayana*, *Ipomea aquatica* and sinuously connected floating grassy mats, that are anchored in some places by a rhizome. These floating grassy mats predominantly consist of the grass species *Leersia hexandra*, *Hymenachne acutigluma*, *Imperata cylindrica, Miscanthus* sp. and emergent sedges like *Scleria sumatrensis*, *S. terrestris*, and *Cyperus* sp. (Giesen & Dommain, 2012). The disturbance of Danau Mesangat over several decades by fires during El Niño events in the 1980s (Chokkalingam et al., 2005) facilitated the invasion of exotic species, which thrive in the area. The most widespread of these are the floating weeds *E. crassipes* and *S. cucullata*, hardy shrubs and grasses, invertebrates like the apple snail (*Pomacea canaliculata*) and vertebrates such as the South American catfish (*Plecostomus* sp.), African tilapia (*Oreochromis mossambicus*) and the giant snakehead (*Channa micropeltes*). The exuberant growth of the invasive aquatic weeds has led to the clogging of waterways and decreased water depths within the wetland, limiting access to locations formerly open during 2009–2011.

Oil palm plantation development in the Danau Mesangat area commenced in 2008 when a local company (PT. Cipta Davia Mandiri, or CDM) received a land lease (HGU) for development of the area for oil palm. Local conservation bodies such as the Yayasan Ulin (Ironwood Foundation), the Conservation Department of PT.REA Kaltim Plantations, a CDM associated company have campaigned for the entire wetland to be conserved. They were joined in 2013 by another NGO, the Equator Conservation Foundation of Indonesia (YASIWA) and a consortium of local government agencies and village officials to protect the area as an Essential Ecosystem Area (Kawasan Ekosistem Essential, or KEE). Plantation development stopped in late 2017, leaving most of the wetland intact.

Population studies. Data were collected during two field visits to the Mesangat wetlands in 2010 in the rainy season (28 October–4 December 2010) and 2011 in the dry season (22 July–22 September 2011). Abiotic data were measured by an automated weather station (Davis Instruments, Vantage Pro 2) installed at a survey raft within Danau Mesangat. Measurements included daily rainfall (mm), air temperature (°C), air pressure (hPa), humidity (%), wind speed (m/s) and water temperature. Moon phases were recorded for the exact location with the Online Software "CalSky"(http://www.calsky.com) to assess whether there was a correlation with crocodile activity. A moon index was defined and calculated for every survey day as the product of the moon phase (lunar phases converted into a scale between 0 for new moon and 1 for full moon) and the moonshine-time in minutes during survey period. The correlation coefficient (Spearman Rank Correlation) between moon index and encounter rate for crocodiles was determined using R (Version 2.10.1). Forest habitats were excluded from the analysis because moonlight was less able to penetrate through the canopy and was not expected to have a significant influence on crocodile sightings.

Surveys were carried out nightly and the locations varied to ensure two consecutive surveys did not occur within the same area. Distribution maps were generated using the ESRI software "ArcGIS" (Version 10.1). A total of 130 nightly spotlight surveys were completed in Danau Mesangat, using a 3–4 m long non-motorised canoe-like boat ("perahu"). Surveys lasted from five to six hours, between 2100 to 0300 hours. A survey team consisted of two people, one seated in the front using a headlight (Zweibrüder 7498 LED Lense H7R, 170 lm, 180 m range) to detect crocodile eye shine and one person in the rear manoeuvring the boat using a bamboo pole or paddle. Spotlight surveys covered a route between 6 and 10 km, with a total area of approximately 20 km^2 searched throughout both field visits.

For each crocodile encounter the species was determined and if possible, the individual was caught by hand. For each individual, whether captured or not, the location of the sighting was recorded (using a hand-held Magellan Triton 400 GPS unit) and the total length of the crocodile was estimated. Crocodiles were categorised into four size classes: "hatchling" (<30cm), "juvenile" (30–80cm), "sub- adult" (80–180cm) and "adult" (>180cm). If an individual submerged before a size could be recorded, it was listed as "*C. siamensis*" (CS), if the species could not be identified it was classified as "eye shine only" (ESO). As *T. schlegelii* are known from the wetland, for population size estimates all ESOs were evenly split between *T. schlegelii* and *C. siamensis*, and if ESOs were uneven numbers the result was rounded to the next higher

whole number in favour of *C. siamensis*. Habitat descriptions of the immediate surroundings for each sighting were also recorded, divided into the categories: "*Salvinia cucullata*" (a floating invasive weed), "floating grassy mat" (a floating mat predominantly consisting of sedges and grasses), "open water" and "forest".

The total body length of captured crocodiles was limited to approximately 1.20 m because of constraints related to the strength of the researchers, the stability of the boat and the safety of its occupants. Outside of formal surveys, in the Abang and Long Balau locations, individual crocodiles were unintentionally caught by local fishermen on hooked fishing lines. For a small compensation, the fishermen provided these animals for examination before the crocodiles were released. All captured crocodiles, whether hand-captured or provided by fishermen, were measured for total length, snout-vent length, head length and width using a tape measure (±1 mm) and callipers (±0.01 mm). Weight was determined using a portable electronic scale (Balzer, ±0.01 kg) and each individual crocodile was fitted with a Passive Integrated Transponder (PIT tag), inserted subcutaneously in the left shoulder. Tail scutes were also cut, to ensure an alternative method for identification (Fig. 2). After examination the animals were released at their original capture site. To estimate the population size of *C. siamensis* in Danau Mesangat, three approaches were used to provide the most comprehensive results.

Firstly, a conservative minimum population estimate of *C. siamensis* was determined for each survey location by counting all clearly distinguishable individuals. For that purpose, the highest number of observed individuals per survey night throughout all surveys was determined for each survey location. The minimum number was adjusted for locations where more individuals have been captured or could be clearly distinguished through the size estimation. ESOs were only included in the calculation, were they could clearly be distinguished from other individuals. This approach was used to avoid double counting.

In order to estimate the total population size of *C. siamensis* in Danau Mesangat, secondly, the mark and recapture analysis was used for individuals marked in 2010 and recaptured in 2011, and calculated using the Peterson-Lincoln method (Lettink & Armstrong, 2003). It was assumed that the Mesangat population was closed, that means, there were no additions (immigration or hatching) or losses (emigration or death) of individuals during the study. Additionally, it was presumed that no PIT tags were lost and that every animal had an equal probability of being captured. To ensure the equal probability of being captured, the population size estimates included only individuals caught accidently on fishing hooks and hand-captures were excluded. The population size estimates were made for locations where *C. siamensis* individuals were caught and extrapolated to include locations where *C. siamensis* had been observed (estimated using Magellan Vantage Point v.2.27 from documented survey routes and satellite images). It was also assumed that the population density was equal across all locations included in the calculation.

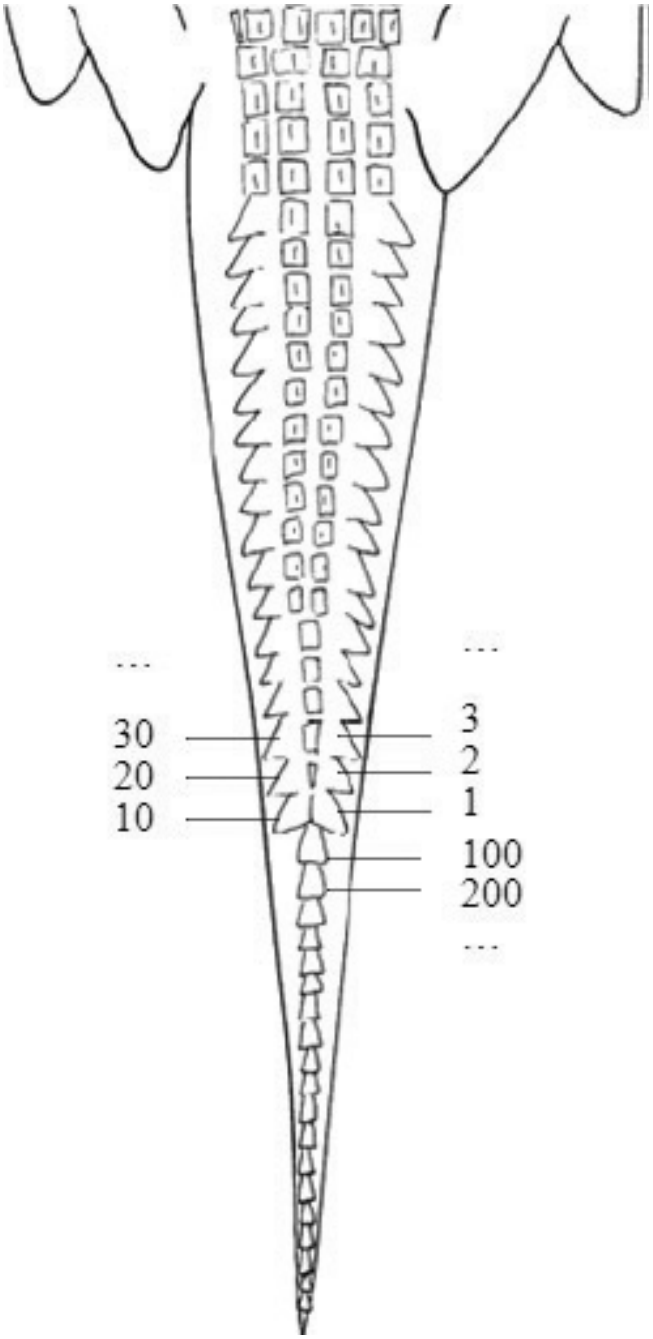

Fig. 2. Code for cut tail scutes on *Crocodylus siamensis* in Danau Mesangat (modified after Kay, 2004).

An additional third population estimation approach was used, established by Webb et al. (1989) for *Crocodylus porosus* and further developed by Bezuijen et al. (2013) to be more suitable for the densely vegetated habitat in which *C. Siamensis* occurs. The minimum population number is multiplied with a correction factor for spotlight counts. For dense habitats such as Danau Mesangat, a correction factor not less than 3 is appropriate (Bezuijen et al., 2013).

Nesting. A targeted search for nests was carried out, based on known locations of old nesting sites, provided by local fishermen. For each nest the geographic location, surrounding habitat, total number of eggs, egg length, width and circumference (vertically and horizontally) was

Table 1. Overview of the minimum number of *Crocodylus siamensis* individuals in the Mesangat wetland and its survey locations in 2010 and 2011. CS = *C. siamensis*; Captured = number of individuals captured; Surveys = number of individuals encountered during surveys; Detected = number of individuals detected and distinguished by estimated total length; ESO-CS (eye shine attributed to *C. siamensis*) = ESO (eye shine only) additionally detected during surveys and divided by two (rounded to whole numbers), but without size class data; Size classes = breakdown of the distinguishable individuals by size classes from the larger group of Captured and Detected column; Minimum number = sum of breakdown by size classes and distinguishable ESO-CS.

Location	CS Captured	CS Surveys		Size classes of Captured/Detected			Minimum number
		Detected	ESO-CS	Juvenile 30–80cm	Sub-adult 80–180cm	Adult >180cm	
Raft	1		0	1	0	0	**1**
Abang	2	5	3	1	2	2	**8**
Abang Hilir		2	1	0	1	1	**3**
Loah Toh		6	0	1	4	1	**6**
Long Balau	9	2	1	4	5	0	**9**
Long Pudau		1	4	0	0	1	**5**
Long Putu		4	0	0	2	2	**4**
Nusa Palong		1	2	0	1	0	**3**
Senyun		3	1	3	0	0	**4**
Total	12	24	12	10	15	7	**43**

Note that no hatchlings were seen during surveys.

determined. Habitat (floating grassy mats), nesting materials and egg sizes were used to distinguish *C. siamensis* nests from sympatric *T. schlegelii* nests.

Diet. The stomach contents of 13 *C. siamensis* were analysed individually according to the procedures from Fitzgerald (1989) and Villegas & Schmitter-Soto (2008). To access stomach contents a PVC pipe with a 2 cm diameter was inserted into the mouth to keep it open and the mouth held in place with a rubber band. A flexible plastic tube with a 6 mm diameter and a smooth tip moistened with cooking oil, was then guided into the oesophagus to the point of its juncture with the stomach. The portion of the tube outside the mouth was connected to a bottle from which water was introduced into the stomach. Once the stomach had perceived to be filled with water the animal was held upside down over a bucket, and a slight pressure applied to the abdomen expelling the stomach contents. The process was repeated until only clear liquid was expelled. The stomach contents were sieved through a fine strainer to remove excess water. The method did not harm the animals and produced essentially complete stomach content samples. The wet weight of the contents was obtained using an electronic balance (Radwag WTB 2000; ±0.01 g). The gastric contents were then fixed in 5% formalin and the coarse components analysed and photographed (Nikon D5000). For analysis, the coarse components were sorted into categories and dried under a laboratory fume hood. The dry mass of the respective portions were weighed using a Sartorius BP110S electronic balance (±0.0001 g). The contents were then classified into prey categories: insects, snails (shell), fish parts, snake scales, bird feathers, small mammal hair, plant material, stones and unidentifiable. The presence of parasitic nematodes was also recorded. Detailed photographs were taken through a microscope (Olympus BX41, Olympus DP21) to ensure accurate identification. A statistical analysis of the contents of each sample was carried out using the non-parametric Friedman test in R (Version 2.10.1).

RESULTS

Population estimate. First, a conservative minimum *C. siamensis* population size of 43 was determined for all surveyed locations of Danau Mesangat by combining the highest number of sightings in a single survey at each location (including surveyed and captured individuals) (Table 1). This is the absolute minimum number of *C. siamensis* seen, therefore it is likely that the population is considerably larger. The total body length of 32 individuals was either estimated during surveys or measured from 12 captured individuals, consisting of 10 juveniles, 15 sub-adults, and seven adults (Table 1).

Second, to estimate population size, the capture-recapture method according to Peterson-Lincoln (Lettink & Armstrong, 2003) was calculated, based on the number of captured individuals by fishermen each year for the Long Balau and Abang locations covering a combined area of 0.565 km^2.

In 2010 a total of six individuals were captured, fitted with PIT tags and marked using tail-scute codes (Fig. 2). One individual was caught again within the same year. Hand captures included, in 2011 a total of nine individuals were captured, six of which were marked. One individual was recaptured in the same year twice and another individual was recaptured in the same year three times. Overall, three individuals that were marked in 2010 were recaptured in 2011 (Table 2).

Considering the area of Long Balau and Abang only,

Table 2. Captured Siamese crocodiles. Recaptured individuals have the same letter. Sc.-No. = Tail-scute number, TL = Total length, SVL = Snout vent length, W = weight, * Individuals captured by hand.

Date	Area	Individual	PIT Tag-No. 9820001610-	Sc.-No.	TL [cm]	SVL [cm]	W [kg]
06.11.2010	Long Balau	A	10300	2	95	48	2.37
12.11.2010	Long Balau	B	09266	30	59	29	0.43
25.11.2010	Long Balau	C	08868	200	77	39	1.23
26.11.2010	Long Balau	D	09225	4	87	44	1.73
26.11.2010	Long Balau	E	13397	5	88	43	1.8
30.11.2010	Long Balau	F	12523	6	80	40	1.15
04.12.2010	Long Balau	F	12523	6	–	–	1.2
29.06.2011	Long Balau	G	09940	202	66	32	0.6
29.06.2011	Long Balau	H	12436	300	88	42	1.35
29.06.2011	Long Balau	F	12523	6	88	44	1.4
30.06.2011	Long Balau	I	10510	302	68	33	0.65
30.06.2011	Long Balau	C	08868	200	94	47	1.95
01.07.2011	At raft	J	08677	303	87	43	1.4
02.07.2011	Long Balau	H	12436	300	–	–	–
03.07.2011	Long Balau	C	08868	200	–	–	2.05
06.08.2011	Abang	K	10376	203	99	49	2.83
07.08.2011 *	Abang	L	12549	–	ca.75	–	–
13.08.2011	Long Balau	D	09225	4	113	56	4.4
20.09.2011 *	Long Balau	C	08868	200	106	54	4.49

the capture-recapture calculation results in an estimated population density of 28 individuals per km^2. Extrapolated to consider the area of all locations where *C. siamensis* occurrence had been verified by nightly sightings, an overall area of approximately 1.847 km^2, the population consists of an estimated number of 52 individuals (less than 120 cm total body length). The body size compositions from 2010 and 2011 showed that individuals smaller than 120 cm make up approximately 69% of the population. Therefore, extrapolating the population size to include all size classes, the total non-hatchling population size for these verified locations was estimated to be around 75 individuals. Furthermore, using the population estimation approach from Webb et al. (1989) and Bezuijen et al. (2013) for a highly vegetated habitat, the population size for the surveyed areas would be around 130 individuals.

Growth rates. The capture-recapture approach also allowed the growth rate and weight gain of three captured individuals to be analysed (Table 2). Animal C was measured three times and grew a total of 29.4 cm within 299 days resulting in a total growth rate of 0.1 cm/day. Individual D grew a total of 25.7 cm in 260 days with a growth rate of 0.1 cm/day. In comparison, animal F grew by 2.5 cm over a time span of 242 days resulting in a total growth rate of 0.03 cm/day.

Nesting. In November 2010, a nest discovered on a floating grassy mat in Long Balau was analysed. The nest consisted of plant material, which was layered up to 1 m high with a width of 165 cm. The eggs were rotten due to previous flooding however, they could still be measured. The interior clutch measured approximately 350 mm, containing 29 eggs. The mean egg length was 85 mm with a range of 80–95 mm, while the average egg width was 53 mm, ranging between 48 mm and 60 mm. The eggs had an average circumference of 185 mm (±5 mm). The nest was identified as a *C. siamensis* nest by the egg measurements, which corresponded to the results of other studies and differed from egg sizes of the sympatric *T. schlegelii* (Bezuijen et al., 1998; Ross et al., 1998). Interviewed fishermen confirmed nest sightings in Abang Hilir, Abang, Long Pudau, and Sekgoy (Fig. 1). According to the locals, breeding *C. siamensis* were sighted most frequently between March and May. All *C. siamensis* nests at Danau Mesangat have been on floating mats of vegetation.

Habitat studies. Overall, *C. siamensis* were detected 77 times during the nightly surveys in both field visits (including repeat sightings). On average 0.6 individuals were sighted per survey and the medium encounter rate was one. Ninety-one percent (91%) of *C. siamensis* were sighted directly adjacent to, or nearby (< 2 m distance), a floating grassy mat, of which 92% were directly within floating vegetation and 8% were found in open water. A total of 8% of all sighted *C. siamensis* were seen in the flooded forest. The moonlight had a significant impact on crocodile sightings, as the encounter rate of crocodiles was significantly inversely correlated with the moon index, with fewer individuals recorded during full moon compared with new moon (Spearman Rank Correlation: $\rho = -0.894$, $p = <0.001$) (Fig. 3).

Diet. The 13 analysed stomach contents were obtained from individuals with an average total length of 86 cm, ranging between 59 and 113 cm. The collected samples contained various prey components, namely insect remnants, snail

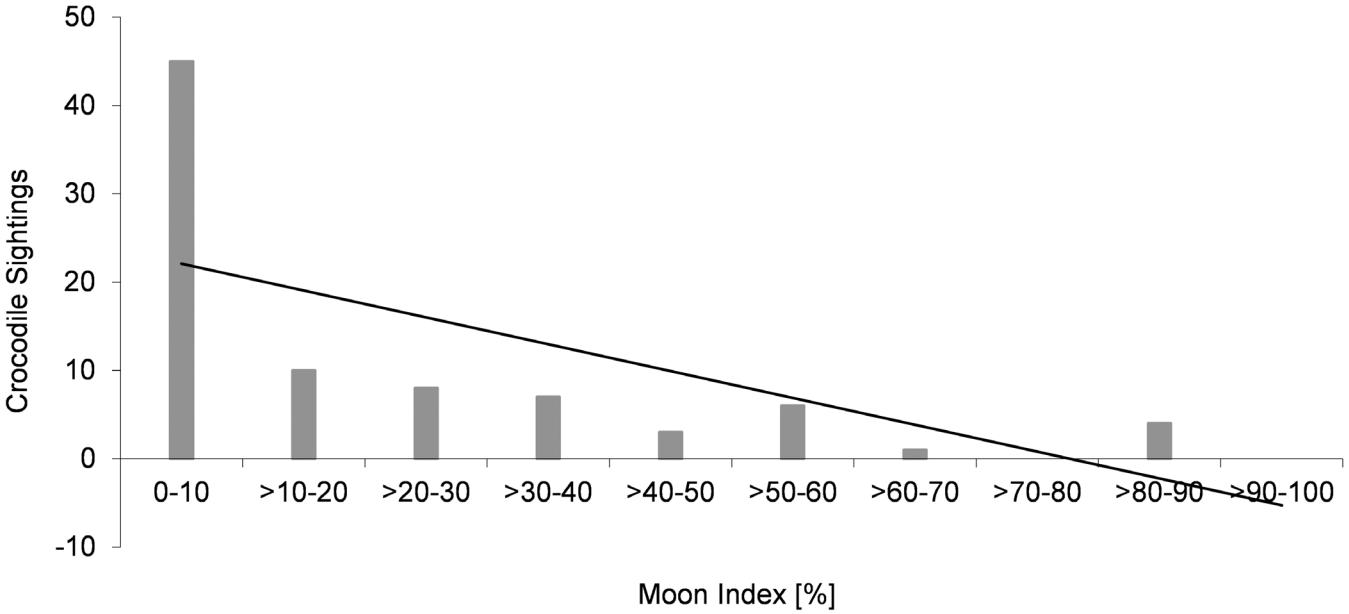

Fig. 3. Correlation between total *Crocodylus siamensis* sightings and moon index.

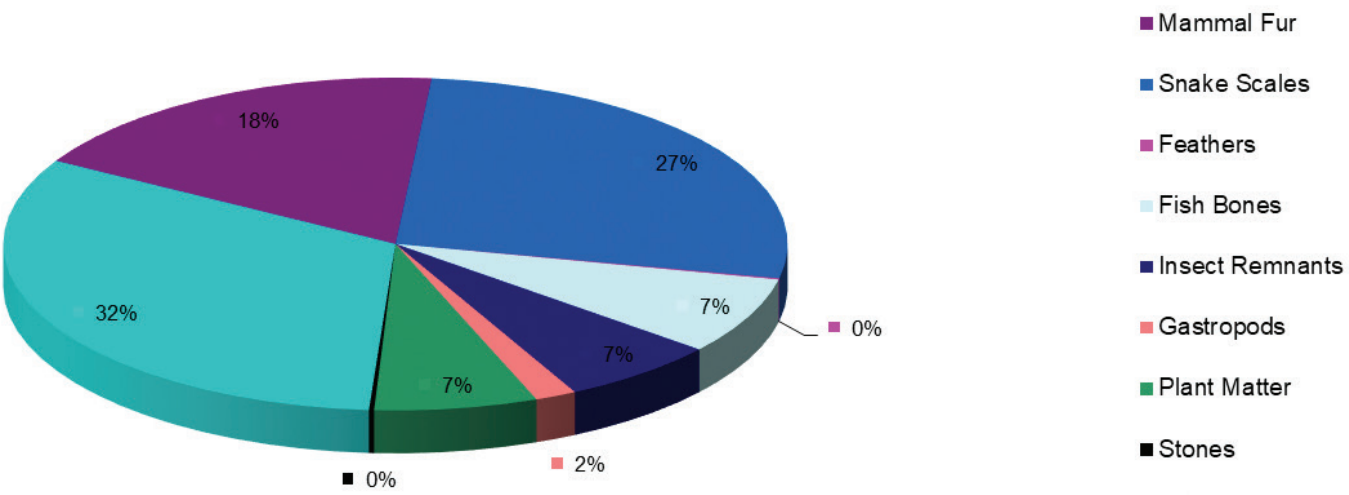

Fig. 4. Relative dry weight of each prey category found in all 13 samples of stomach lavages from *Crocodylus siamensis*.

shells, fish bones, bird feathers, snake scales and small mammal fur (Fig. 4). There was a significant difference in the dry masses of the various prey components (Friedman test: $\chi^2 = 38.27$, df = 7, p = 0.003). Snake scales made up the largest proportion of the dry mass of all samples (27%), followed by mammal hair (18%). The 'other' category consisted of components that could not be clearly identified or assigned to another category. To calculate the difference in the dry mass components of each sample, the 'other' category was omitted. Fig. 4 illustrates a breakdown of the dry mass components of each sample. There were differences in the compilation of the separate samples. Sample 2 contained mainly insect remnants while the dry mass of sample 12 was dominated by snake scales. Nematodes were discovered in eight out of the 13 stomach contents. Plant material and insect remnants were found in all 13 samples, while fish bones were recognised in nine samples. Mammal fur was discovered in eight samples and snake scales in five. Further analysis of the mammal fur showed that at least eight different species of mammal were consumed, one of which was most likely a representative of the Muridae (rat) family. Sample 5 contained necrophagic ants.

Threats. Currently, the greatest threat to the Mesangat crocodile population is the gradual sedimentation and senescence (see Lindeman, 1941) of the wetland resulting in excessive weed growth. Based on recent reports by local fishermen, unless the original flow rates through the lake are restored, depths at many sites in the wetland continue to decrease, with a progressive reduction in the depth of portions of the lake. Another serious threat to *C. siamensis* is potential habitat loss from plantation development. Among the hazards to the survival of the species from plantation development are siltation from land clearing for planting and infrastructure, potential draining (by means of massive pumps) of inundated areas, and runoff from heavy use of inorganic fertilisers that promote and intensify oil palm fruit production. Local communities have in the past been another source of stress on the *C. siamensis* population until the 1990s with some locals harvesting *C. siamensis* hides (Local fisherman Bapak Yus, pers. comm.) for sale to local buyers. No significant harvest of *C. siamensis* has been recorded from Danau Mesangat for at least a decade.

Crocodiles inadvertently caught on fishing hooks are released immediately (Local fisherman Bapak Yus, pers. comm.), although local subsistence fishermen are known to opportunistically collect eggs from nests (including those of the sympatric *T. schlegelii*) if they discover them. A few individuals of the species may still be held in crocodile farms near Samarinda and Balikpapan.

DISCUSSION

In Danau Mesangat, around 80% of all *C. siamensis* sightings were juveniles or sub-adults. This is generally in agreement with the population composition of other species such as *C. johnstoni* and *C. porosus* (Webb et al., 1989). In general, juveniles and sub-adults may have been sighted more frequently because these size classes are easier to detect or more approachable (Webb et al., 1979; Bayliss et al., 1986). In addition, double counting of individuals may have occurred, biasing the population composition results. Age and total length do not necessarily correlate in crocodilians (Hutton, 1987; Halliday & Varrel, 1988) and the chosen categories describing length (size classes) are subjectively divided into hatchlings, juveniles, sub-adults and adults (Webb et al., 1989). In this study, the growth rate of caught individuals ranged from 0.03 cm to 0.1 cm per day, which indicates that body size does not directly correlate to age. An alternative explanation for the varying growth rate may be a difference between males and females and a change in growth rate with age. As observed by Sah & Stuebing (1996) in Western Sabah (Malaysia), *C. porosus* hatchlings grew between 0.01 and 0.08 cm per day while juveniles grew at a minimum daily rate of 0.11 cm.

Adult *C. siamensis* may also have been spotted less frequently than juveniles due to increased competition between fully-grown individuals and increased wariness of the older adults (Webb et al., 1979; Bayliss et al., 1986). Adults were detected in five different locations in Danau Mesangat (Long Pudau, Loah Toh, Long Putu, Abang, and Abang Hilir). Predominantly only one or two adults were spotted at each site simultaneously, which may indicate territorial behaviour of adult *C. siamensis*. (Table 1). *Crocodylus siamensis* are known to be social and exhibit biparental care (Brueggen, 2002), however details of their territorial behaviour in the wild have not been sufficiently investigated.

Overall, the estimated number of around 75 individuals in Danau Mesangat is lower than the known population size in Cambodia, recorded as 200–400 individuals (Simpson & Bezuijen, 2010; Sam et al., 2015) and higher than the recorded population in Laos of at least 36 individuals (Bezuijen et al., 2013). As adult crocodiles are harder to detect than juveniles (Webb et al., 1979), the population size may be significantly larger than estimated and the results may be biased towards sub-adults. Using the estimation approach originally developed by Webb et al. (1989) and used by Bezuijen et al. (2013), our cautious estimate of 130 individuals in Danau Mesangat slightly exceeds the estimation of 100 individuals for Laos. Caution is certainly required since correction factors were originally developed for different species and habitat types (Webb et al., 1989; Bezuijen et al., 2013). However, the Mesangat population, since it is concentrated at one site, may comprise the largest healthy, integrated population known within its original distribution in Southeast Asia. Cambodia's population is scattered and consists of many isolated individuals over 35 different sites throughout the country, with the largest connected population estimated to be approximately 40 individuals in Veal Veng Marsh (Sam et al., 2015).

In this study, the capture-recapture analysis is rather imprecise due to the small sample size and the long time period over which captures were counted. Furthermore, the assumption of having a closed population may be untrue. Webb et al. (1989) report that 50% of freshly hatched Australian freshwater crocodiles (*Crocodylus johnstoni*) survive the first two months and the mortality rate in their first year lies at 88%. However, no new hatchlings were sighted between 2010 and 2011 and the dominant habitat (forested habitat with floating vegetation in open areas) may affect the movement of individuals within the habitat. In addition, the population density may not be evenly distributed across all survey locations. Nevertheless, at least seven adults between 200 and 400 cm total length could be distinguished in five different locations during spotlight surveys (Table 1). Additionally, the minimum number of 43 individuals, in combination with the high ratio between captured individuals and those actually seen in Long Balau (Table 1), may be an indicator for a considerably larger population size.

Furthermore, a nest discovered in 2010 and regular reports of hatchlings and nesting in at least five separate locations by local fishermen support the likelihood that the Mesangat population is relatively stable and supported by ongoing reproductive success. The size of the eggs are consistent with other studies on *C. siamensis* eggs and are easily distinguished from the much larger eggs of the sympatric *T. schlegelii*, which are up to 106 mm long and 65 mm wide (Bezuijen et al., 1998, Ross et al., 1998). In addition, fishermen have reported that individuals prefer erecting nests in the same location every year, which indicates a loyalty of individuals to a specific nesting area.

Moreover, since research activity has only recently commenced in Mesangat and adjacent wetlands, it is highly likely that *C. siamensis* occupies a larger area than could be surveyed in this study, thus possibly supporting a more generous estimate of its population size. Wijayanti et al. (2017) describe 80 km^2 of the whole Mesangat wetland as open water and floating vegetation with grass wetland, which is the typical habitat, where most of the *C. siamensis* sightings occurred during this research effort. Based on the estimation of around 75 individuals in a survey area of 20 km^2, there may be up to 300 non-hatchling individuals in the entire area of the Mesangat lake. This extrapolation is comparable to the number estimated for Cambodia of 200–400 individuals (Simpson & Bezuijen, 2010; Sam et al., 2015) but it is very speculative, as three quarters of the Mesangat habitat could not be accessed and surveyed. Although migration is affected by the surrounding feature of landscape, it is not impossible,

especially during high water season. Migration to nearby locations could be stimulated by competitive behaviour of adult individuals. Therefore, further investigation in Danau Mesangat and adjacent wetlands may be a promising intention and is required to further clarify the population size and status of *C. siamensis* in East Kalimantan.

The influence of the moonlight noted on the detection rate of *C. siamensis* individuals can be explained by the increased detectability of the researchers themselves during brighter nights by the crocodiles. Sarkis-Gonçalves et al. (2004) found a similar correlation for *Caiman latirostris* in Brazil. This finding improves planning future nightly surveys more effectively and economically.

The stomach content analyses of *Crocodylus siamensis* in Danau Mesangat prove that the species feeds on a wide range of prey items available in the habitat, demonstrating a generalist predation strategy. These findings are consistent with faeces analysis from Laos (Bezuijen, 2010) and Cambodia (Sam et al., 2015). All analysed stomach contents contained plant material, which may be an indication of purposeful consumption, although Hernandez (1983) stated that plant matter has no biological importance in crocodilian diets. Throughout this study the majority of individuals were found near floating grassy mats, which makes the accidental consumption of plant matter during hunting another possibility. The secondary consumption of the plant matter through the stomach contents of consumed prey can be eliminated as an explanation since the particle size of consumed plants frequently exceeded that of other consumed prey (for example in sample 13).

Previous analyses of *C. johnstoni* and *C. porosus* stomach contents also included significant quantities of plant matter. In *C. johnstoni* 39.9% of samples contained plant material, while 43.8% of the samples contained parasite infestation (Webb et al., 1982). A study by Sah & Stuebing (1996) discovered that 75% of *C. porosus* stomach samples contained plant materials and parasites were rarely encountered, most likely related to the saltwater habitat of the species. In comparison, nematodes were present in 62% of the Mesangat samples. The presence of necrophagic ants in one sample, if not secondarily ingested, may be an indicator of scavenging behaviour in *C. siamensis*, since ants have been observed on carrion in the field. Sam et al. (2015) found that *C. siamensis* in Cambodia consumed carrion and Daltry et al. (2003) reported approximately 30 ants in one *C. siamensis* faeces sample.

Amphibians were absent from all stomach samples, although abundant in the study area. An explanation would be their easy digestibility described by Daltry et al. (2003). In contrast, insect remnants were found in all samples, most likely because chitin is not easily digestible and therefore remains more or less intact in the stomach (Bezuijen, 2010; Sam et al., 2015).

The significant variation in dry weight of the various prey categories may indicate the species' preference for certain prey, however the varying degrees of decomposition and digestibility make this theory difficult to prove. Multiple factors may affect the validity of the stomach contents analysis. A total of 11 of the 13 samples originated from the inadvertent capture of crocodiles by fishermen. Since fish are used as bait, the samples cannot be considered independent. In addition, studies by Magnusson et al. (1987) and Webb et al. (1982) have discovered fundamental differences in the diet composition of different size classes of different crocodile species. The results of this study are therefore only applicable to juveniles and sub-adults in the size range 59–113 cm. Furthermore, the analysis may only be valid for the Mesangat wetland since Taylor (1979) was able to show that diet composition and body condition of *C. porosus* depends on their habitat. Overall, the reliability and significance of a quantitative analysis of the individual weight of various prey components remains in question. The qualitative approach to analysing stomach contents is far more useful in determining *C. siamensis* diet.

This study was able to estimate population size, describe demography, determine habitat use and give an insight into the diet of juvenile and sub-adult *C. siamensis* in Danau Mesangat. Further investigation is needed to fully document and understand the ecology as well as other aspects of the biology of the species in this area. This is becoming more important to focus conservation efforts amidst increased threats to the limited number of viable wild populations of *C. siamensis*.

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