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Clutch splitting and nesting behaviour of the Eastern Malay River Terrapin, *Batagur affinis edwardmolli* Praschag et al., 2009, in Malaysia

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Five of the six sandbank-nesting river turtles of the genus *Batagur*, including both subspecies of the Southern River Terrapin, *Batagur affinis* (Cantor, 1847), are critically endangered and listed among the world's freshwater turtles at highest risk of extinction (Stanford et al., 2025). Long-term exploitation of eggs for human consumption remains a major threat to these communally nesting species. Nesting sandbanks have been heavily exploited for centuries (Maxwell, 1911, referring to *Batagur baska* [Gray, 1831] and *Batagur trivittata* [Duméril & Bibron, 1835]; Moll and Moll, 2004), and in Malaysia there are currently no known *B. affinis* nesting sites where females can nest without human presence (Pan, 1988; Chan et al., 2008; Chan and Chen, 2011; Chen, 2017).

During the nesting season, egg collectors often outnumber nesting females, resulting in intense competition to locate nests and intercept nesting turtles. To counteract egg loss, conservation programmes for *B. affinis* in Malaysia rely heavily on nest protection or translocation, hatchery incubation, captive breeding, and the release of head-started juveniles. Despite decades of sustained intervention, these measures alone have not yet halted population declines (Moll and Moll, 2004; Moll et al., 2015; Chen, 2017), and monitoring of nesting females remains a central component of management.

An implicit assumption underlying many monitoring protocols is that oviposition is complete when a female leaves the nesting area. In most aquatic turtles, the entire clutch is deposited into a single nest cavity during one nesting event, with only occasional retention of individual eggs (Kuchling, 1999). However, clutch splitting into multiple nest holes is well documented in *Batagur affinis edwardmolli* Praschag et al., 2009 and *Batagur trivittata*. Females of *B. a. edwardmolli* may divide a clutch among multiple nest holes (up to four) within a single night (Moll and Moll, 2004; Moll et al., 2015) or on separate nights (Chen, 2018), although available evidence suggests that spreading clutch deposition over more than one night is uncommon under undisturbed conditions. *Batagur trivittata* consistently deposits clutches into multiple nest holes during the same nesting event or night (Win Win Mar, 2007). This strategy is thought to reduce the risk of total clutch loss to predation and, during mass nesting events as they occurred in the past, may also reduce the risk of other females unearthing and destroying the eggs of a whole clutch. The only other turtles reported to also use comparable nesting strategies are several taxa in the genus *Pseudemys,* which dig three-holed nests (one main egg chamber and two adjacent shallow "false nests" in which up to two eggs may be laid), and occasionally *Apalone mutica,* which may divide one clutch into more than one nest cavity (Moll and Moll, 2004). Clutch splitting has not been described for the large, mass-nesting South American river turtles in the genus *Podocnemis* or the arribada-nesting sea turtles of the genus *Lepidochelys*.

Given this nesting strategy, interpreting nest counts and clutch sizes requires confidence that oviposition has been completed. In this note, we present observations from the Kemaman River suggesting that apparent completion of nesting does not necessarily coincide with completion of oviposition of a clutch in *B. affinis*, and that post-nesting interception of females may bias clutch size estimates and interpretations of nesting behaviour.

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Materials and Methods

This pilot study formed part of a broader project on the reproductive ecology of *Batagur affinis edwardmolli* conducted on the east coast state of Terengganu, Peninsular Malaysia. Fieldwork was carried out at one of the nesting sandbanks of the species in the Kemaman River which is approximately 250 m long and up to 30 m wide (name and location withheld for security reasons). Nesting activity was monitored from February to March over three consecutive years (2012–2014).

Field observations were conducted by the authors together with five local villagers. During each nesting night, the sandbank was patrolled at approximately hourly intervals beginning between 20:00–20:30 h and continuing until nesting activity had ceased. Nesting females were observed until they had completed covering and camouflaging their nest holes. Here, a nest hole refers to a single excavation containing eggs, whereas a nesting event may include the construction of multiple nest holes before the female returns to the river. When a female showed signs of returning to the river, she was captured by hand and transported to a nearby campsite for morphometric measurements and passive integrated transponder (PIT) microchip insertion.

To examine whether post-nesting capture coincided with completion of oviposition, between 14–19 February 2013 five females intercepted after apparent nesting completion were screened for the presence of retained oviducal eggs using portable ultrasonography. Ultrasound examinations were conducted with a Toshiba Sonolayer-L SAL-32B unit equipped with a 5-MHz linear array probe, powered by a vehicle battery. Due to the large body size of the females and the limited visual field of the equipment, ultrasound screening was exploratory and intended to determine only the presence or absence of oviducal eggs, rather than to quantify egg number.

We base the assumption that eggs laid in separate nights were part of previously partly laid clutches on the general knowledge of oviducal periods of turtles. Many turtles lay multiple clutches per nesting season based on additional ovulations following the deposition of the previous clutch. Nesting intervals of multi-clutch species give an indication of oviducal periods which generally last from nine days at the low end (leatherback turtle) to about a month and occasionally longer (Kuchling, 1999). It is, thus, unlikely that females of any turtle species nesting across multiple nights in shorter intervals than about a week deposit separately ovulated clutches. Moll (1990, in Moll et al., 2015) observed a wild female *B. affinis affinis* from the Kedah River laying two clutches (24 and 29 eggs) separated by a two-week interval. Since clutch splitting has not been described in this subspecies, we assume the normal oviducal period of *B. affinis* (excluding eggs retained for longer) may be about two weeks or slightly less. We consider all eggs laid in between eight days of a previous nesting event to belong to the same clutch of eggs and not to a separately ovulated egg clutch.

Results

Ultrasound scanning detected that all five post-nesting *Batagur affinis edwardmolli* females still had eggs in their oviducts (Table 1), but only two of them were observed returning to nest subsequently. After laying the initial nest containing nine eggs, female C returned five days later to lay two more nests containing 21 eggs. Female C laid a total of 30 eggs. Female D laid 12 eggs in the first nest and returned twice subsequently to lay three more nests containing 27 eggs for a total of 39 eggs.

The clutch size for *B. a. edwardmolli* was estimated from the number of eggs recorded on all nesting events during this study (Table 2). Females that deposited their eggs over three nesting events, hence assumed to have completed nesting, recorded the largest mean clutch size with 29.75 ± 6.29 eggs ($n = 4$, range, 25–39). This assumption was based on repeated observations that total egg counts plateaued after three nesting events, with no subsequent oviposition detected. Comparatively, females that nested during one and two nesting events deposited between 20.7–21.0 eggs, and were assumed to have laid only partial clutches. A gradually declining trend was observed in females that deposited their eggs in more than one nest hole on one and two nesting events.

Females were only intercepted and brought back to the campsite after what seemed like an attempt to return to the river. Seven females proceeded to dig a second and third nest before showing signs of returning to the river, hence they were left on the nesting bank to complete nesting before they were captured (two females in 2012, four females in 2013 and one female in 2014). Assuming that these females had completed nesting in the same night, the mean clutch size for these nests is 24.57 ± 4.47 ($n = 7$, range, 20–33).

Discussion

Completion of nesting was inferred in our study from

Table 1. The nesting pattern of five *Batagur affinis edwardmolli* females examined by ultrasound scanning after their first nesting event in the Kemaman River, Terengganu, Malaysia.

Female	Date Of First Nesting, Number Of Nest Holes/ Eggs Per Hole (Comments)	Ultrasound Detection Of Oviducal Eggs	Re-emergence Date, Number Of Nest Holes/ Eggs	Additional Nesting Dates/ Holes/ Eggs	Total Number Of Eggs Deposited
A	14/15Feb2013 1st: 11 eggs	Yes	?		11 - partial clutch
B	14/15Feb2013 1st: 8 eggs	Yes			8 - partial clutch
C	17/18Feb2013 1st: 9 eggs (uninterrupted)	Yes	22/23Feb2013 2nd: 11 eggs 3rd: 10 eggs		30 - full clutch?
D	18/19Feb2013 1st: 12 eggs 2nd: 0 egg	Yes	21/22Feb2013 3rd: 12 eggs 4th: 8 eggs	01/02Mar2013* 5th: 7 eggs	39 - full clutch?
E	19/20Feb2013 1st: 9 eggs 2nd: 11 eggs	Yes	?		20 - partial clutch

* Since the interval between the 4th and the 5th nest hole was 8 days but that of the 1st and the 5th nest hole 11 days, the possibility cannot be excluded that the 7 eggs of the 5th nest hole were part of a subsequently ovulated separate clutch if its ovulation occurred after the first night of nesting. However, we consider this unlikely since, after the first nesting night, at least 20 eggs of the clutch were retained until the second nesting night.

Table 2. Estimated clutch size of *Batagur affinis edwardmolli* females spreading nesting over one, two or three nesting events from 2012 to 2014 in the Kemaman River, Terengganu, Malaysia. Values are given as mean ± standard deviation.

	Number Of Eggs In The 1st Nest Hole	Number Of Eggs In The 2nd Nest Hole	Number Of Eggs In The 3rd Nest Hole	Number Of Eggs In The 4th Nest Hole	Total Number Of Eggs
One nesting event	10.86 ± 2.92 *n* = 29	8.66 ± 3.18 *n* = 29	4.86 ± 1.77 *n* = 7		20.69 ± 5.52
Two nesting events	10.86 ± 2.32 *n* = 22	8.86 ± 3.55 *n* = 22	6.20 ± 2.59 *n* = 5		21.05 ± 4.80
Three nesting events	10.60 ± 1.95 *n* = 5	10.50 ± 1.91 *n* = 4	5.50 ± 3.00 *n* = 4	6.00 ± 1.41 *n* = 2	29.75 ± 6.29

repeated nesting events and total egg counts rather than from behavioural cues alone. A general nesting strategy of *Batagur affinis edwardmolli* and *B. trivittata* appears to involve splitting a single clutch among multiple nest holes (Tables 1, 3). This strategy complicates the use of nesting observations and egg counts in nests to estimate clutch size in these species (Table 3). In some early studies, each nest hole was treated as representing a separate clutch (Maxwell, 1911; Holloway, 2003), leading to underestimation of true clutch size. Even when clutch splitting is recognised and nests are examined the morning after nesting (Win Win Mar, 2007), nest holes may be overlooked or cannot be confidently assigned to individual females when multiple turtles nest on the same sandbank during a single night, as occurred historically during mass nesting events (Maxwell, 1911). Although, apart from *B. a. edwardmolli* and *B. trivittata*, we are not aware of descriptions of clutch splitting in other large-bodied sandbank nesting taxa in the genus *Batagur,* without checking egg retention in post-nesting females, this can easily be overlooked.

Direct observation of nesting females followed by post-nesting capture for identification and morphometric measurements, as conducted in this study, presents a trade-off between data collection and behavioural interference. Ultrasound screening showed that none of the five examined females had completed oviposition at the time of capture, indicating behavioural cues commonly used to infer nesting completion may be unreliable at least in *B. a. edwardmolli* (Table 1). Consequently, reproductive assessments based on this approach are likely to underestimate clutch size.

Table 3. Mean clutch size and range of complete and partial clutches of *Batagur affinis* and *Batagur trivittata*. AMNH = American Museum of Natural History.

Species	Mean Clutch Size	*N*	Range	Location/ Comments	Reference
B. affinis affinis	-	-	20–50	Perak River	Loch, 1950
	-	-	13–34	Perak River	Balasingam and Mohamed Khan, 1969
	26.4	231	5–38	Perak River	Moll, 1980
	-	2	24–29	Kedah River	Moll, 1990
B. affinis edwardmolli	42.5	2	42–43	Terengganu River, complete clutches from several holes	Moll et al., 2015
	14 (partial)	36	4–32	Terengganu River, single nest holes	Moll et al., 2015
	-	8	3–19	Sre Ambal River, Cambodia	Holloway, 2003
	26.9	132	7–43	Setiu River, females were captured before nesting and entire clutches were laid in a secret location	Chan and Chen, 2011
	29.8	4	25–39	Kemaman River, 3–4 nest holes laid in three nesting events	This study
	21.3 (partial)	69	10–33	Kemaman River	This study
B. trivittata	36	1	36	Oviducal eggs of AMNH R58559, coll. 14 March 1935	Kuchling, unpubl. data
	35.5	21	18–58	2–8 nest holes, laid in same night	Win Win Mar, 2007

Although our data indicate that splitting clutches among several nest holes is a common nesting strategy in the Kemaman River *B. affinis edwardmolli* population, it remains unclear whether deposition of a single clutch across multiple nesting events on different nights represents normal behaviour. Available evidence suggests that this pattern is uncommon. Additional observations from the Kuantan River in Pahang, approximately 40 km south of the Kemaman River (straight-line distance) support this interpretation. On two occasions, undisturbed females deposited eggs into two nest holes during a single nesting night and did not return to nest again until 16 days later, a pattern consistent with deposition of separate clutches rather than continued oviposition of a single clutch. Because the females were not individually marked, it is unclear whether the same or different individuals were involved; nevertheless, the long inter-nesting interval supports interpretation of these events as separate clutches (Chen et al., 2026). Previous studies of *B. affinis edwardmolli* in the Terengganu River reported clutch splitting into up to three nest holes within a single night, but did not document clutch deposition spread over multiple nights (Moll, 1980; Moll et al., 2015). Similarly, the most comprehensive nesting study of any *Batagur* species, *B. trivittata*, found no indication that oviposition extends across multiple nights, despite clutches being divided among multiple nest holes (up to eight) during a single nesting event (Win Win Mar, 2007). Repeated terrestrial nesting events may also increase exposure of these highly aquatic turtles to terrestrial predators, making such behaviour unlikely under undisturbed conditions. The re-appearance of females later during the same night or on subsequent nights observed in this study is therefore consistent with a response to conditions on the sandbank, including ongoing human activity and perceived risk.

These nesting strategies complicate clutch size assessment based solely on egg counts in nests. Variation in clutch size among females is expected, and the presence of few eggs in a nest or nest hole does not necessarily indicate interrupted oviposition. The mean clutch size estimated for apparently completely deposited clutches in this study (29.8) is comparable to the mean clutch size of 26.9 eggs recorded in the Setiu River (Table 3), where females were captured before nesting and transported to a secluded location to complete oviposition (Chan and Chen, 2011). In that study, the annual mean clutch sizes ranged from 23.4 to 30.1 eggs. In several instances during the present study, females were only captured after depositing three nest holes within a single night, suggesting that complete oviposition can occur when disturbance of nesting females is delayed.

The most accurate determination of clutch size in *Batagur* would involve radiographic examination or

dissection of gravid females prior to nesting. To our knowledge, radiography has not been applied to these species, and dissection is now clearly inappropriate for critically endangered turtles. Nevertheless, a gravid *B. trivittata* female (AMNH R58559) collected during the Vernay–Hopwood expedition in 1935 over 90 years ago (Morris, 1936) contained 36 oviducal eggs (Table 3). This value is consistent with the mean clutch size of 35.48 eggs recorded from complete clutches deposited into multiple nest holes by undisturbed *B. trivittata* females along the upper Chindwin River (Win Win Mar, 2007). Two *B. affinis edwardmolli* clutches deposited into three nest holes within a single night contained 42 and 43 eggs, respectively (Moll et al., 2015; see Table 3), substantially exceeding clutch size estimates based solely on egg counts in nests of females intercepted on nesting sandbanks.

In contemporary Malaysian populations, nesting without human presence is rare, limiting opportunities to observe undisturbed oviposition. Females in this study were intercepted after they appeared to have completed nesting and were returning to the river, but it is possible that oviposition would have continued in the absence of human observers. Alternatively, females may have perceived the sandbank as insecure and temporarily abandoned nesting, returning later to deposit remaining eggs. Such disturbance may prompt females to shift to adjacent or less suitable sandbanks, as suggested by telemetry data from a post-nesting female that spent approximately one hour on a neighbouring nesting bank, presumably to deposit remaining eggs (Chen and Wong, 2015). Nesting at suboptimal sites could reduce hatching success and undermine conservation objectives.

Taken together, ultrasound screening and nesting observations from the Kemaman River indicate that *B. affinis edwardmolli* routinely divides clutches among multiple nest holes and that apparent completion of nesting based on behavioural observations does not necessarily correspond to completion of oviposition. Intermittent return to the water and spreading deposition of one clutch over several nights and/or sandbanks is possibly not a normal pattern, but may be caused by the disturbance of nesting females by human observers. At least in this subspecies, nesting completion can be difficult to interpret and standard monitoring methods may underestimate clutch size. To minimise bias in clutch size estimation and reduce potential disruption to nesting behaviour, conservation programmes may benefit from limiting direct interaction with females during nesting and prioritising non-invasive observation where feasible.

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