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Natural history of three freshwater turtle species within two logging reserves in Sabah, Malaysian Borneo

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Abstract. Asian freshwater turtles are severely threatened by overharvesting for local and international trade. Whilst some research exists on their occurrence in market places, basic studies on their natural history are scarce. Effective conservation action requires an understanding of both the threats to a species and its ecology. Our research aims to elucidate some basic aspects of the natural history of three freshwater turtle species: *Notochelys platynota*, *Heosemys spinosa* and *Dogania subplana* in Sabah, Malaysian Borneo. We collected opportunistic turtle data within two logging concessions from 2017 to 2019, and conducted dedicated turtle sampling via Visual Encounter Surveys (VES) along rivers in 2019. These data were used to determine population characteristics, habitat associations/separation, movements, recapture rates, breeding behaviour, and parasitism. We obtained 157, 40 and 13 records of *N. platynota*, *D. subplana* and *H. spinosa,* respectively. Roughly equal adult/juvenile ratios were detected in two species, whereas adults predominated (2.6:1) in *N. platynota*. Both *N. platynota* and *H. spinosa* exhibited similar sex ratios, with significant sexual dimorphism (males larger than females) in *N. platynota*. *Notochelys platynota* and *D. subplana* were significantly associated with wider streams compared to *H. spinosa*, whilst *D. subplana* were significantly associated with higher relative siltation than *N. platynota*. Recapture rates of *N. platynota* were low (N = 12), with recaptured *N. platynota* movements ranging from 10–489 meters. High rates of parasitism by freshwater leeches (*Placobdelloides siamensis*) were identified in *N. platynota* (41% of VES detections, N = 50), whilst 30% of *H. spinosa* were infested with ticks (N = 3). The effects of high parasitism on *N. platynota* require further study, however we observed a large breeding population of *N. platynota* in the logging reserves examined. Habitat separation between these three species at fine spatial scales, via stream width and siltation, likely permits their co-occurrence along the same stream networks. We recommend the protection of heterogeneous stream networks to improve effective conservation measures for these species.

Key words. Testudines, *Notochelys platynota*, *Heosemys spinosa*, *Dogania subplana,* population dynamics, habitat separation, parasitism, recapture rates.

Introduction

Asian freshwater turtles are currently suffering massive regional declines, mostly driven by unsustainable harvesting for the international food and pet trade (Cheung & Dudgeon 2006, Gong et al. 2009). Whilst China constitutes the largest trade market, Southeast Asia is the primary source of harvested turtles, which due to the region's high turtle diversity and local endemism is a major cause for concern (Bour 2008, Rhodin et al. 2017). Overharvesting is exacerbated by habitat disturbance/loss, urbanisation and hydro-electric dam development in the region (Van Dijk 2000). Despite the pressing need for Asian freshwater turtle conservation action, surprisingly little is known concerning the natural history of most species in the wild. The majority of recent studies have focused on market surveys and quantifying the scale of the international trade, particularly in China (Cheung & Dudgeon 2006, Gong et al. 2009, Van Dijk 2000). As a result, little data on basic population dynamics, habitat associations, and natural history are available for many species. This is primarily attributed to the difficulties in sampling freshwater turtles due to their scarcity, low detectability, and occurrence in difficult-to-survey aquatic habitats. Most ecological turtle studies from the region have therefore either focused on the population dynamics of more common/widespread species (Schoppe

2008), or provide overviews of turtle diversity (Ibrahim et al. 2018). This is particularly troubling in areas with high turtle diversity and land conversion rates.

The island of Borneo contains twelve understudied freshwater turtle species and is subject to some of the highest land conversion rates in Asia (Struebig et al. 2015). More than half of these turtles species are classified as Threatened by the IUCN (Rhodin et al. 2017). Three of these, the Spiny hill turtle *Heosemys spinosa* (Gray, 1831), Malayan flat-shelled turtle *Notochelys platynota* (Gray, 1834), and the Malayan soft-shell turtle *Dogania subplana* (Geoffroy Saint-Hilaire, 1809), are harvested throughout Borneo for local food markets (Jensen 2006, Jensen & Das 2008a, Walter 2000) and the international trade, predominantly with China (Cheung & Dudgeon 2006, Gong et al. 2009). As a result, *N. platynota* and *H. spinosa* are listed as Vulnerable and Endangered, respectively, whilst the relatively common *D. subplana* is listed as Least Concern by the IUCN. These species occupy small stream networks in forested habitats throughout Southeast Asia (Lim & Das 1999). *Dogania subplana* and *H. spinosa* are purportedly found within clear fast-flowing hill streams, whereas *N. platynota* is associated with shallow, slow–flowing, sandy-bottomed streams (Ibrahim 2018, Lim & Das 1999). As most freshwater turtle studies focus on larger water bodies, species occupying smaller watercourses are often understudied.

In the present study, we used incidental observations made over three years and dedicated turtle sampling in one year to elucidate factors relating to the natural history of these three freshwater turtle species. Specifically we provide data for: i) population characteristics: detections and measurements, ii) habitat associations/separation, iii) recaptures and movements, iv) parasitism rates and possible predation attempts, and v) possible breeding behaviour and hatchlings.

Materials and methods

Data for this project were collected both incidentally during a herpetofauna monitoring project (Asad et al. 2020, Asad et al. 2021) and from dedicated turtle sampling within the Deramakot and Tangkulap Forest Reserves (Fig. 1). The reserves comprise hilly, lowland dipterocarp forests (50–350 m a.s.l) at varying stages of regeneration following reduced-impact (Deramakot) and conventional selective logging (Tangkulap). Herpetofauna monitoring covered 39 stream and 11 terrestrial sites (100 metres in length each) in both reserves, surveyed using Standardized Visual Transect Survey (SVTS) methods. Eight Visual Encounter Survey (VES) sites (1100–2850 metres in length) were used for dedicated turtle sampling in Deramakot only. Stream and terrestrial transects were visited on 3–17 occasions between March and June in 2017, 2018 and 2019, whereas three visits to dedicated turtle VES sites occurred between March and June 2019. Stream/terrestrial transects were surveyed at 3.3 m per minute, whereas VES sampling involved greater survey speeds (20–40 m per minute). All data were collected by two observers between 18:30 and 23:30 hrs. In both survey types, all freshwater turtles were identified to species level following Lim & Das (1999). Additionally, GPS location, time of capture, sex, adult/juvenile status, curved carapace/straight plastron lengths, par-

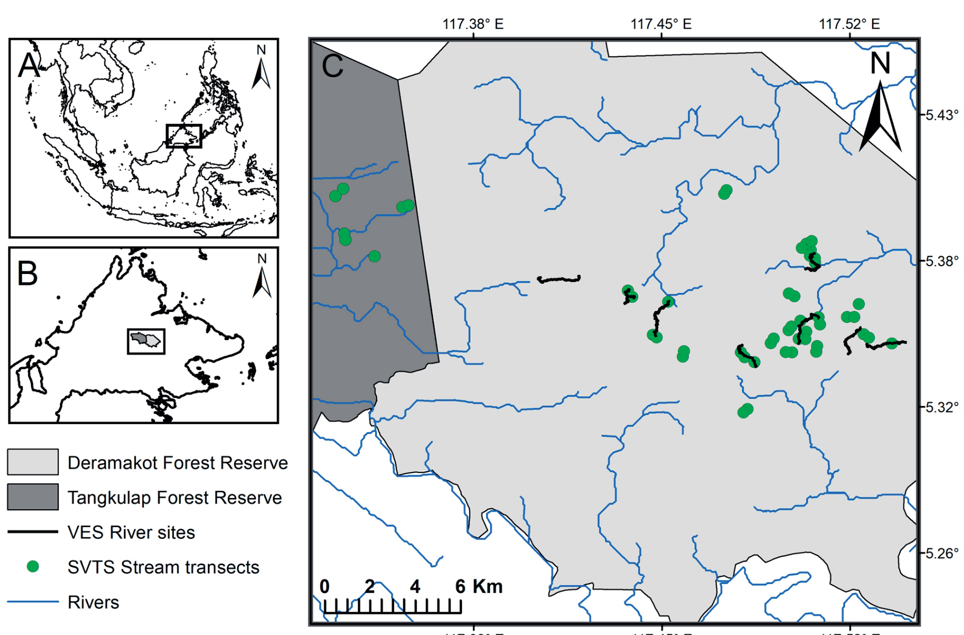

Figure 1. Map of (A) Location of Sabah, Malaysian Borneo, in Southeast Asia, (B) Location of the Deramakot and Tangkulap Forest Reserves in Sabah, (C) Location of our Visual Encounter Survey (VES) river sites and Standardized Visual Transect Survey (SVTS) stream transect locations in both reserves.

asite burden, and behavioural observations were recorded. In order to avoid injuries, the soft-shelled turtles were neither measured nor sexed. Stream width was measured at all turtle capture locations, whilst stream depth and siltation were recorded during VES only. Stream widths and depths were recorded as the widest distance between banks and deepest points of the river where a turtle was located. We visually assessed siltation in the stream within a 2 m radius of the turtle's location, classified as 0–25, 26–50, 51–75 and 76–100% siltation cover.

Analysis of variation in female and male carapace/plastron lengths was conducted using unpaired two-sample Wilcoxon tests. Kruskall-Wallis tests were used to determine if significant variation exists between stream widths for all three species, followed by unpaired two-sample Wilcoxon tests between species. Unpaired two-sample Wilcoxon tests were used to determine whether significant variation exists between *N. platynota* and *D. subplana* siltation and stream depth. To determine if significant variation in parasite prevalence occurred between adults/juveniles and females/males we conducted Chi-square tests of independence. All analyses and subsequent graphs were produced with the software R version 4.0.2 (R Core Team 2019).

Results

Population characteristics: detections and measurements

Between March 2017 and June 2019, we recorded 210 observations of the study species, with most detections occurring during the dedicated VES turtle sampling (N = 159). *Notochelys platynota* was by far the most commonly detected species over both the three-year study period and during the dedicated turtle sampling (N = 157 and 127, respectively), followed by *D. subplana* (N = 40 and 30) and *H. spinosa* (N = 13 and 1). Adult:juvenile ratios in this population of *N. platynota* (adults: 112, juveniles: 45, ratio: 2.6:1) and *H. spinosa* (adults: 9, juveniles: 4, ratio: 1.8:1) were high, whereas adult:juvenile ratios were more balanced in *D. subplana* (adults: 21, juveniles: 19, ratio: 1.1:1). The male:female ratio in both hard-shelled species was fairly balanced in *N. platynota* = (males: 61, females: 41, ratio: 1.2:1) and *H. spinosa* (males: 3, females: 3, ratio: 1:1).

Significant sexual dimorphism was recorded in *N. platynota* (curved carapace: W = 213.5, $p < 0.0005$ and plastron: W = 211.5, $p < 0.0005$), with males being larger (N = 58, curved carapace: 295.2 ± 25.8 mm, plastron: 224.6 ± 33.5 mm) than females (N = 49, curved carapace: 221.5 ± 44.4 mm, plastron: 175.2 ± 17.4 mm) (Fig. 2). *Heosemys spinosa* curved carapace and plastron length was larger in males (N = 3, 199.2 ± 43.9 mm, 165.2 ± 4.3 mm) than in females (N = 3, 168 ± 39.9, 138.3 ± 24.1), however sample sizes were too small to confirm significant sexual size dimorphism (Fig. 2).

Habitat associations/separation

We found significant differences between the stream dynamics associated with each species. Both *N. platynota* and *D. subplana* occurred in large to moderately sized streams (*N. platynota* = 154, streams = 15, stream width: 452.5 ± 160 cm; *D. subplana* = 39, streams = 13, stream width: 390 ± 182 cm), whereas *H. spinosa* were associated with significantly smaller, narrower streams (*H. spinosa* = 9, streams = 5, stream width: 124.7 ± 60.8 cm) (Fig. 3). Furthermore, compared to *N. platynota* and *D. subplana*, *H. spinosa* were generally detected in more sloped and rocky streams. *Notochelys platynota* and *D. subplana* occupied streams of similar width and depth, but differed in their associations with stream siltation (Fig. 3). *Dogania subplana* was significantly positively associated with more heavily silted streams (*D. subplana* = 30, streams = 7, siltation: 64 ± 26%) than *N. platynota* (*N. platynota* = 127, streams = 8, siltation: 50 ± 19%) (Fig. 3). Furthermore, *D. subplana* was frequently found burrowing in heavy siltation deposits (Fig. 4A).

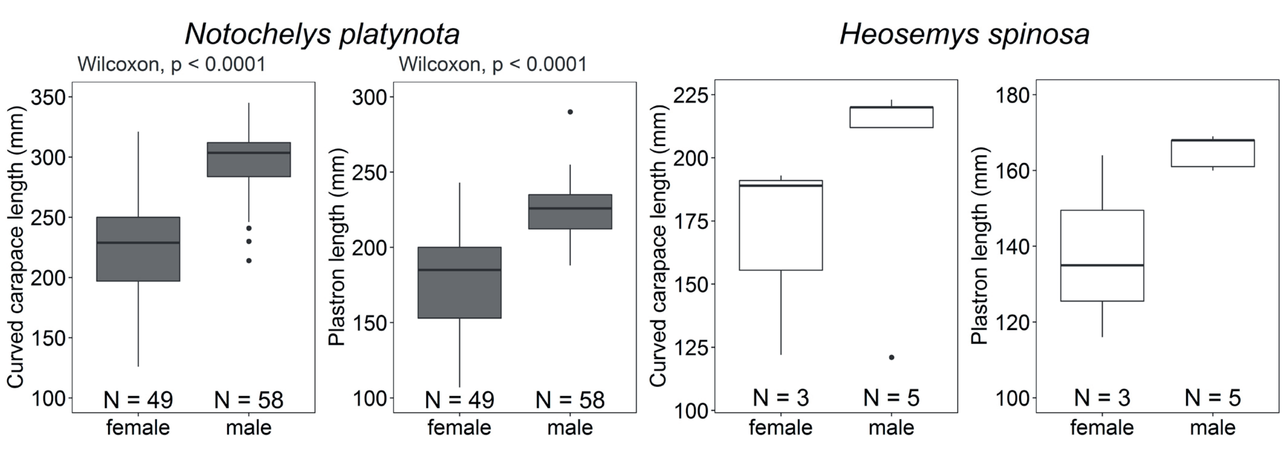

Figure 2. Plastron and curved carapace length of female and male *Notochelys platynota* and *Heosemys spinosa*. Sample sizes of each turtle species and the results of unpaired two-sample Wilcoxon tests for *N. platynota* are provided.

Table 1. *Notochelys platynota* and *Heosemys spinosa* recapture and movement data. Sex/life history stage, curved carapace and plastron lengths are given for all recaptured individuals, including curved carapace and plastron lengths for specimens recaptured > 180 days after the initial capture.

Species	Sex/life stage	Length (mm)		Days until recaptures		Total movement (metres)	Length at recapture (mm)	
		Carapace	Plastron	1st	2nd		Carapace	Plastron
Notochelys platynota	Male	290	210	45	–	47	–	–
	Male	310	235	1	356	489	317	242
	Juvenile	73	61	42	260	10	90	67
	Female	150	117	27	–	30	–	–
	Female	215	172	21	–	96	–	–
	Female	211	164	24	–	14	–	–
	Male	304	218	51	–	66	–	–
	Male	281	213	54	–	90	–	–
	Female	235	194	54	–	68	–	–
Heosemys spinosa	Male	223	169	9	53	10	–	–

Terrestrial observations of all three species were rare, with one observation of *N. platynota* and *D. subplana* each, and three terrestrial observations of the same *H. spinosa* individual. The *N. platynota* and *D. subplana* observations were made separately along a main road with the respective individuals appearing to be crossing it on their way to aquatic habitats. The *H. spinosa* was recaptured at the same location along an old logging trail on three occasions within two months.

Recaptures and movement

Using the unique markings on the plastra of *N. platynota* and *H. spinosa*, we were able to identify several subsequently recaptured individuals. We detected 145 individual *N. platynota*, with twelve recaptures made of nine individuals, and eleven individual *H. spinosa*, with three recaptures of one male (Table 1). The recaptured *H. spinosa* was exclusively detected terrestrially, on an old logging trail, within 10 m of the original capture location over a two-month period. *Notochelys platynota* recaptures were within 10–489 m of initial capture locations within the same rivers (Table 1). Whilst the mean straight-line distance between captures was 101 ± 148.6 m, the high standard deviation is the result of a single 489 m movement by a large male (curved carapace: 310, plastron: 235 mm) between 2018 and 2019 (Fig. 5). During this period (357 days), this male's curved carapace and plastron length had increased by 7 mm. Only one juvenile (curved carapace: 73, plastron: 61 mm) *N. platynota* was also recaptured in both 2018 and 2019, within 10 m of the initial capture location. This juvenile's curved carapace length had increased by 17 mm and its plastron length by 6 mm. All remaining recaptures occurred within a period of 1–2 months.

As recapture rates for *N. platynota* were low, reliable density estimates for the two reserves could not be inferred. At two rivers however, recaptures of three and one adult *N. platynota* respectively over the VES period allowed for a rough estimation of density using the Lincoln-Petersen estimator (Menkens jr. & Anderson 1988). This indicated that these two rivers had a density of roughly 4.3 and 7.8 adult turtles per kilometre, respectively.

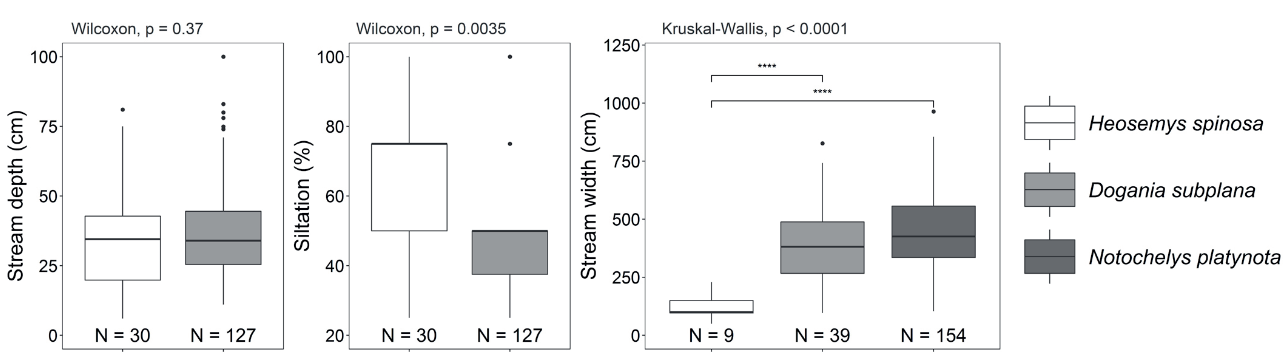

Figure 3. Stream measurements at capture locations of the three turtle species, including stream depth, siltation, and stream width. Sample sizes of each species and the results of Kruskal-Wallis tests and unpaired two sample Wilcoxon tests are provided.

Parasitism and possible predation attempts

Parasitism by freshwater leeches appeared to be common within this population of *N. platynota*, with leeches detected on the plastra of 41% of turtles recorded during VES (N = 50; Figs. 4B, 6). No statistically significant variations in leech prevalence between adults and juveniles (Chi^2 = 0.37, p = 0.54) or between males and females (Chi^2 = 0.09, p = 0.75) were identified. However, juveniles exhibited a slightly higher leech prevalence than adults (44.7 and 38.3% respectively), and a we observed a slightly prevalence in males than females (40.8 and 35.1% respectively) (Fig. 6). The highest density of freshwater leeches was found on a large adult male (N = 15). Additionally, unidentified nema-

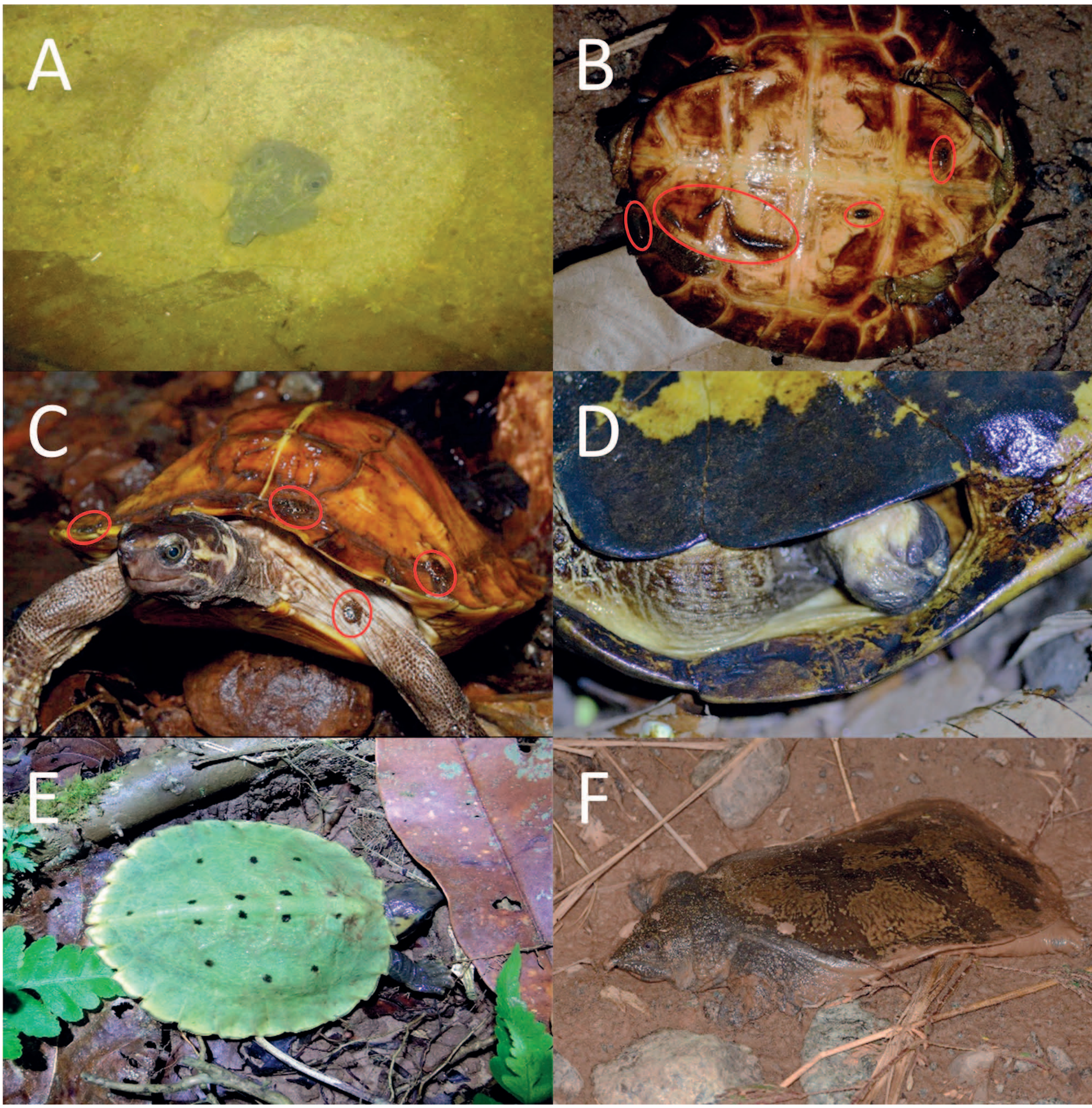

Figure 4. Photographs of notable turtle observations; (A) *Dogania subplana* submerged in the sand of a stream bed, in a possible ambush or antipredation position (16 May 2019, 20:11 h); (B) parasitism of *Notochelys platynota* by freshwater leeches (likely *Placobdelloides siamensis*) circled in red (03 May 2019, 19:26 h); (C) parasitism of *Heosemys spinosa* by ticks (possibly an *Amblyomma* species) circled in red (17 June 2019, 21:21 h); (D) *Notochelys platynota* with a missing left hind limb (08 April 2019, 19:46 h); (E) a recent *Notochelys platynota* hatchling (curved carapace = 60 mm, plastron length = 38 mm) (31 March 2018, 22:03 h), (F) a *Dogania subplana* individual on a main road away from water sources (11 September 2017, between 19:00 and 22:00 h).

todes were found in the faeces of five *N. platynota* (1 adult female, 4 juveniles). Whilst leeches and nematodes were not detected in *D. subplana* or *H. spinosa*, ticks were observed on several *H. spinosa* (Fig. 4C). These ticks were found attached to the carapaces and necks of three individuals (one female, male and juvenile), representing almost a third of all detected *H. spinosa*.

During VES, we detected six *N. platynota* individuals (four males and two females) with missing limbs, representing 5% of all *N. platynota* observed during these surveys (Fig. 4D). In all cases, one entire foot was missing, and occasionally a significant portion of the respective leg, too.

Possible breeding behaviour and hatchlings

During VES, five observations of *N. platynota* in aggregations were made on three survey occasions (28 April, 4 May and 16 May 2019). These aggregations consisted of 3–5 adults of both sexes, located within 3–20 metres of one another. Notably, during one survey (16 May 2019), three such aggregations were documented on a single river (Fig. 7). Additionally, we recorded a number of juveniles, including thirteen hatchling *N. platynota* between March and June in 2018 and 2019. Three hatchlings were recent, with open plastra and bright green carapaces (Fig. 4E).

Other freshwater turtles

During our study, we detected two additional freshwater species, *Cuora amboinensis* (Daudin, 1802) (N = 4) and *Cyclemys dentata* (Gray, 1831) (N = 2). *Cuora amboinensis* were detected in small ponds, within swampy areas, and on main roads, potentially attempting to cross these. Whilst such observations were infrequent, forestry staff members and other researchers purportedly document the latter regularly. *Cyclemys dentata* was detected twice in a moderately sized, slow, highly silted river.

Discussion

Our study provides information on the population characteristics, habitat associations/separation, recapture rates, movements, parasitism, and possible breeding behaviour for three freshwater turtle species within two logging concessions in Sabah, Malaysian Borneo. Whilst data were limited in some cases (*Heosemys spinosa* detections, *Dogania subplana* sexual identity/measurements, *Notochelys platynota* recaptures), our results provide many novel and previously unquantified findings concerning the natural history of these species. As our study took place within conventional selectively and reduced-impact logged forests, our results may not apply to turtle populations living in other undisturbed habitats. We are currently quantifying the effects of these logging types on *N. platynota* and *D. subplana* populations in a separate publication.

Population characteristics: detections and measurements

Within our study site, *Notochelys platynota* was by far the most frequently detected species (N = 157), followed by *Dogania subplana* (N = 40), and with infrequent detections of *Heosemys spinosa* (N = 13). Whilst *H. spinosa* is listed as Endangered and rarely encountered, *D. subplana* is listed as

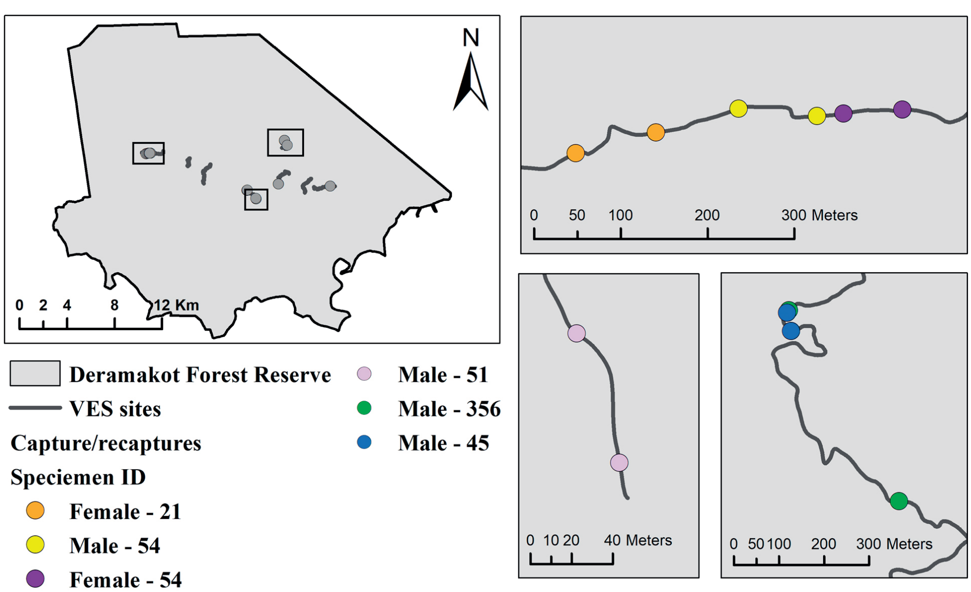

Figure 5. Map of *Notochelys platynota* capture/recapture locations including sex and days until recaptures, and inset maps of recapture locations with more than 30 metres from the initial capture point.

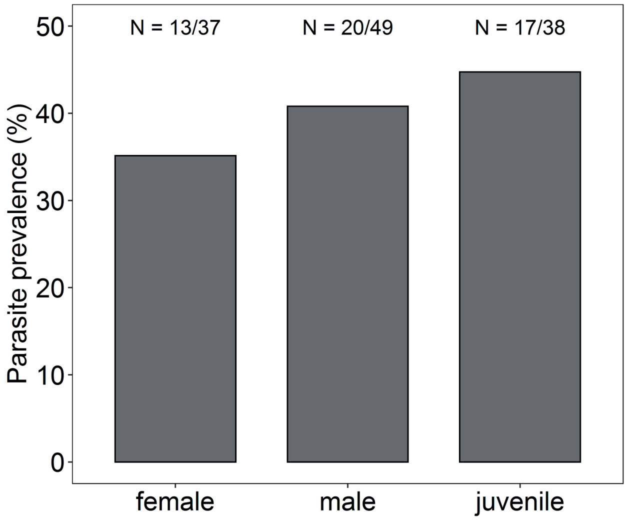

Figure 6. Percentage of female, male and juvenile *Notochelys platynota* individuals parasitized by freshwater leeches (likely *Placobdelloides siamensis*), including the number of parasitized/ total number of *N. platynota* individuals sampled during VESs.

Least Concern and encountered more frequently throughout its range than the Vulnerable *N. platynota* (Ibrahim 2018, Ibrahim et al. 2018, Lim & Das 1999). Whilst our data suggests that *N. platynota* is considerably more common within this area than *D. subplana,* this disparity in detections could be linked to the burrowing habits and therefore possibly lower detection probability of *D. subplana*. Regardless, the high number of detections over the relatively short VES sampling period suggests a relatively large and stable population of *N. platynota* exists at our study sites.

The high adult to juvenile ratio in *N. platynota* within our study site is typical of hard-shelled freshwater turtle species in other regions (Budishak et al. 2006, Mogollones et al. 2010, Spencer 2002). This is likely the result of low juvenile detectability and high juvenile/low adult mortality in long-lived hard-shelled species (Klemens 2000). Although sex was not identified in *D. subplana*, both hard shell species exhibited fairly balanced sex ratios. Whilst sex ratios are often askewed in unsuitable habitats (due to sex-specific mortality), roughly balanced sex ratios indicate suitable conditions and suggest no pressure is exerted on one specific sex in this population (Budishak et al. 2006).

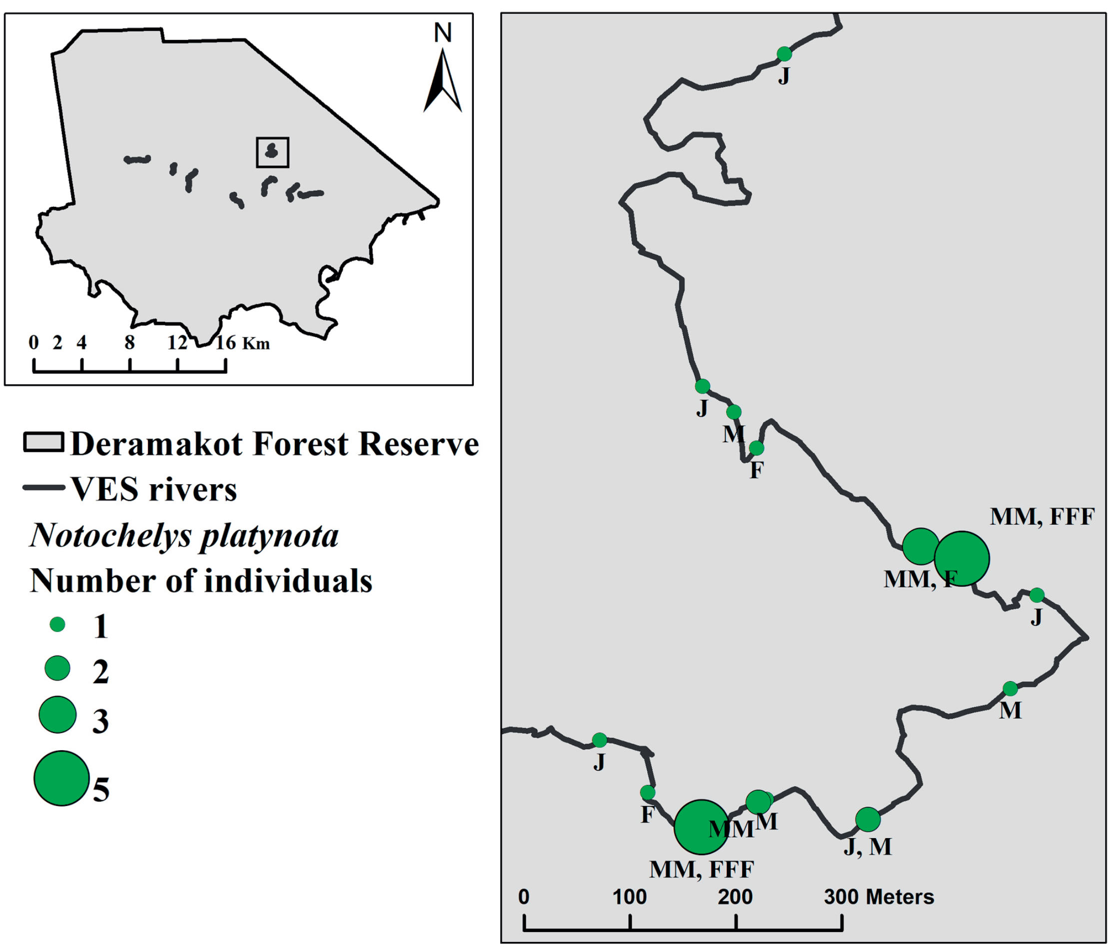

Figure 7. Map of all *Notochelys platynota* detections during a single VES survey (16 May 2019), including locations of aggregations, and sex/life history stage of all detected individuals (male/female/juvenile).

As with previous studies (Brophy & Ernst 2004), we found significant sexual size dimorphism in *N. platynota*, with males being larger than females. The largest female (curved carapace: 321 mm , plastron: 243 mm) and male (curved carapace: 345 mm, plastron: 290 mm) were considerably smaller than the maximum recorded for *N. platynota* elsewhere (carapace length: 360 mm) (Lim & Das 1999). Although sexual size dimorphism in turtles usually favours larger females (Gibbons & Lovich 1990), larger males occur in semi-aquatic, "bottom-walking" turtle species (Berry & Shine 1980). This conforms to our field observations of *N. platynota* behaviour and habitat associations within our study site (see below).

Habitat associations/separation

Whilst our study species were all detected along the same stream networks, there was significant variance in the fine-scale stream dynamics preferred by each species. *Notochelys platynota* and *D. subplana* were associated with wider streams than *H. spinosa*, whilst *D. subplana* was more frequently associated with higher siltation than *N. platynota*. Studies of co-occurring freshwater turtles in wetland and riverine habitats on the Iberian Peninsula and the Americas identified similar fine-scale separation between aquatic habitat associations, yet significant co-occurrence at coarse spatial scales (Anthonysamy et al. 2013, Jaeger & Cobb 2012, Segurado et al. 2012). As with these studies, separation between *H. spinosa, N. platynota* and *D. subplana* by fine-scale stream dynamics (namely stream width and siltation), likely allows these species to occupy the same stream networks without competition. Furthermore, our species likely increase separation by differences in ecology, diet and behaviour. *Notochelys platynota* and *H. spinosa* are predominantly herbivorous with occasional predation and scavenging of carrion (Baizurah & Das 2020, Bonin et al. 2007, Ernst & Barbour 1989, Jensen & Das 2006, Lim & Das 1999, Manthey & Grossmann 1997). Visible plant matter, including the flowers of fruiting dipterocarp trees, was detected in the faeces of many *N. platynota* during our study. *Dogania subplana* on the other hand is more omnivorous (Bonin et al. 2007, Lim & Das 1999, Manthey & Grossmann 1997), and its large head and more posteriorly positioned eyes suggests that molluscs likely constitute a large portion of its diet (Pritchard 2001). Several *D. subplana* were found slowly moving through the submerged leaf litter deposits on the bottom of streams, potentially foraging for the freshwater snails that occupy these microhabitats. Additionally, we detected a large *D. subplana* individual underwater burried in the substrate with only the nose, eyes and mouth protruding (Fig. 4A), in what appeared to be an ambush position, as is commonly reported in soft-shell turtles (Pritchard 2001). This could also have been anti-predation behaviour however as several *D. subplana* fled to the nearest sandy area and quickly burrowed beneath the surface when disturbed.

Our aquatic observations of *N. platynota* (N = 156) and *D. subplana* (N = 39), suggest a predominantly aquatic lifestyle in concordance with the majority of the literature (Bour 2008, Ernst & Barbour 1989, Lim & Das 1999, Manthey & Grossmann 1997, Nutaphand 1979, Rogner 1995). However, aquatic observations of *H. spinosa* (N = 10) contradict many previous records. A range of activity patterns have been reported for *H. spinosa*, including greater terrestrial activity in juveniles (Ernst & Barbour 1989, Rogner 1995), greater terrestrial activity in adults (Goetz 2007), with some authors suggesting the species to be almost entirely terrestrial (Bonin et al. 2007, Nutaphand 1979). Although our total observations are limited (N = 13), we believe the species to be at least semi-aquatic. However, our lower number of detections compared to *N. platynota* and *D. subplana*, terrestrial recaptures, and the detection of ticks on several *H. spinosa* (see Parasitism and possible predation attempts below) indicate a more terrestrial lifestyle than the former two species. Future studies of *H. spinosa* should therefore include surveys of terrestrial and stream habitats to quantify the relative utilisation of these by this little-known species.

Recaptures and movement

During our study we noticed that the plastral markings of *N. platynota* and *H. spinosa* were unique to each individual. The majority of individuals captured were therefore photographed to allow individual recognition and identify recaptures. A single *H. spinosa* was recaptured on an old logging road within 10 m of the initial capture location twice within two months. Previous research by Baizurah (2021) identified predominantly small-scale relocation by radio-tracked *H. spinosa* in Sarawak, which is supported by the localized nature of our *H. spinosa* recaptures.

Whilst the growth rates of two *N. platynota* captured in 2018 and 2019 were fairly high compared to other hard-shelled species (Budishak et al. 2006, Kennett 1996, Martins & Souza 2008), recaptured *N. platynota* moved relatively short distances compared to freshwater turtles from Australia (Bower et al. 2012) and the USA (Rowe 2003, Rowe et al. 2009). As the individuals in our study were not radio-tracked, we cannot confirm whether this was due to limited movements or small home-range size. The single largest *N. platynota* movement over a 356-day period (489 m) is dwarfed by movements of other riverine freshwater turtle species over shorter periods (Bower et al. 2012, Rowe 2003, Rowe et al. 2009). The low recapture rates for this species complicate matters further, as individuals with high site fidelity/smaller home ranges should be expected to be recaptured more frequently (Efford et al. 2016). Reduced recapture rates due to high mobility are therefore questionable in this species. Low recapture rates due to high mortality are also unlikely in view of our detection of many large adults. Low recapture rates are typical in freshwater turtles that experience relatively stable mortality/recruitment rates in other regions (Budishak et al. 2006, Jensen & Das 2008b). The limited number of *N. platynota* recaptures is therefore likely a result of fluctuations in individual/species detectability. Rainfall and seasonality have been identified as factors associated with freshwater turtle activity and thus detectability in Australia, the USA, and Brazil (Anthonysamy et al. 2013, Roe & Georges 2008, Rowe 2003, Rowe et al. 2009, Souza & Abe 1997). Furthermore, a study of freshwater turtles in Sarawak, Malaysian Borneo, identified species-specific activity associations with climatic variables (Jensen & Das 2008b). Accounting for species detectability associations with climatic covariates will be essential for further studies seeking to quantify population dynamics and disturbance effects on *N. platynota* and other freshwater turtle species. Additionally, tentative population density estimates obtained from recapture data at two rivers, indicate a surprisingly low density compared to other riverine freshwater turtle species (Bower et al. 2012, Souza & Abe 1997). As recapture rates were low and detectability unknown, these numbers are likely a severe underestimation. More research and dedicated capture-recapture studies are required to infer more reliable population density estimates.

Parasitism and possible predation attempts

We detected high freshwater leech parasitism within the study population of *N. platynota*. Based on the presence of a distinct yellow dorsal stripe, we believe these freshwater leeches to be *Placobdelloides siamensis* (Oka, 1917), which commonly parasitize freshwater turtles throughout Southeast Asia (Chiangkul et al. 2018, Govedich et al. 2002). Whilst this may represent a new distribution record for *P. siamensis*, specimens were not collected, and so their identity cannot be confirmed. High parasitism by freshwater leeches is a well-documented occurrence in other freshwater turtle populations in the USA (Readel et al. 2008, Ryan & Lambert 2005). Within Southeast Asia, parasitism by *Placobdelloides* species has been recorded from numerous chelonians throughout the region (Chiangkul et al. 2018). Low variance in parasitism rates between sex and age of *N. platynota* suggests both a widespread prevalence of the parasite throughout the site, and similar habitat use and infection rates across sexes and age classes. The negative effects resulting from high infection rates by *Placobdelloides* in this population is so far unknown. Whilst freshwater turtles infested with leeches are typically healthy, heavy infection loads can compromise health and have been associated with higher rates of haemogregarine infections (Davis & Sterrett 2011). Quantifying the effects of leech parasitism on *N. platynota* survival should therefore be considered in further research.

The ticks detected on a number of *H. spinosa* were likely an *Amblyomma* Koch, 1844, species that commonly parasitizes freshwater turtles (including *H. spinosa*) throughout Southeast Asia (Simmons & Burridge 2000). This tick parasitism provides further indications of more terrestrial habits in *H. spinosa* compared to *N. platynota* and *D. subplana*.

The loss of limbs in 5% of the *N. platynota* detected during VES and subsequent healing can possibly be attributed to predation attempts or/and inter-/intraspecific aggression. Freshwater turtles in Borneo (and elsewhere) are thought to be heavily predated upon as juveniles (Lim & Das 1999). Whilst few species would be able to penetrate the thick shell of an adult *N. platynota*, the limbs are relatively unprotected and could be removed by a wide range of Borneo's carnivorous species (Reptiles: *Varanus salvator* (Laurenti, 1786), Mammals: Viviridae, Lutrinae, Sunda clouded leopard *Neofelis diardi* (G. Cuvier, 1823), Sun bear *Helarctos malayanus* (Raffes, 1821) etc.). Aggressive interactions including biting have been documented from various turtle species, e.g., between invasive Red-eared sliders *Trachemys scripta* (Thunberg in Schoepff, 1792) and Spanish terrapins *Mauremys leprosa* (Schweigger, 1812) in Spain (Polo-Cavia et al. 2011), and between four species of emydid turtles in the USA (Lindeman 1999). Furthermore, maiming following both male/male aggression (Keevil et al. 2017) and aggressive sexual coercion (Moldowan et al. 2020) has been documented in other hard-shelled freshwater species. The latter may in some cases result in high female wounding and lower survival (Golubović et al. 2018). Unfortunately, the cause of injuries to the six *N. platynota* individuals can only be speculated upon. However, as these wounds appeared to be old, healed, and the individuals in otherwise good condition, the loss of limbs surprisingly does not seem to compromise their health and survival.

Possible breeding behaviour and hatchlings

The close proximity, mixed sex nature, and temporal fluctuation of the *N. platynota* aggregations we recorded suggest that this may have been some form of breeding aggregation. Whilst aggregations for basking and feeding are common in freshwater turtles (Lindeman 1999, Polo-Cavia et al. 2011, Rovero et al. 1999) such explanations appear unlikely due to the stable thermal environments and even distribution of plant matter within our study site. Spotted turtles *Clemmys guttata* (Schneider, 1792) are known to form site-specific breeding aggregations in Georgia, USA (Enneson & Litzgus 2009). Unfortunately, more behavioural observations of *N. platynota* aggregations are required to confirm if these truly are groups of breeding individuals. Mating in *Notochelys platynota* was only ever observed once (3 April 2019) at our site, with a male mounting a female underwater. Borneo experiences a subtle dry season between May and November (Kitayama et al. 2021), yet we detected female/male aggregations and hatchlings both before and during this period. Although we found no evidence for seasonal breeding/hatchling patterns, our four- to six-month sampling periods are insufficient to confirm or deny a seasonal breeding pattern in this species.

Whilst breeding behaviour/hatchlings were not detected in the two other species, an interesting incidental observation of a single *D. subplana* was made by the side of a road (11 September 2017) (Fig. 4F). This large female appeared to be crossing the road, and although its motives can only be speculated upon, soft-shell turtles in other areas are known to move over land to locate suitable egg-laying sites (Plummer 2007, Xinping et al. 2015).

Conclusion

Our results elucidate important observations on the natural history of *Notochelys platynota*, *Dogania subplana* and *Heosemys spinosa* in the wild. Adult/juvenile and male/female ratios appear to be quite balanced in this population (with the exception of *N. platynota*), and similar to turtle populations in other areas. Despite high parasitism rates in *N. platynota*, we detected many large adults and recent juveniles indicative of a healthy, breeding population in the Deramakot Forest Reserve (despite the prevalence of reduced-impact logging). Individual recognition in this species indicated short, localized movements, which may make these species particularly vulnerable to overharvesting/site-level habitat disturbance. Most importantly, we identified significant variation in the preferred stream dynamics of these three species within the same river systems, indicating a level of fine-scale separation via stream width and siltation in their riverine habitats. It is for these reasons that the preservation of heterogeneous stream habitats should be prioritized for the conservation of these freshwater turtle species.

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