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Possible spatial separation at macro-habitat scales between two congeneric *Psammodynastes* species, including observations of fishing behaviour in *Psammodynastes pictus*

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The mock vipers *Psammodynastes pictus* Günther, 1858 and *Psammodynastes pulverulentus* (Boie, 1827) are relatively common colubrids found throughout South and Southeast Asia (Das 2012). Whilst *P. pulverulentus* is widely distributed from India, China to the Philippines and Indonesia, *P. pictus* has a comparatively restricted distribution, confined to west Malaysia, Singapore, Sumatra and the states of Borneo (Charlton 2020). Scant natural history data exists for this genus, with most studies focusing on *P. pulverulentus*. These suggest that this species is comparatively common compared to other snakes in its range, and is found in pristine and disturbed forests (Miller et al. 2006, Dieckmann et al. 2013). Most observations were made during the day, with *P. pulverulentus* observed cruising the forest floor purportedly hunting (Greene 1989). Nocturnal observations of this snake, usually involve individuals seen resting on low vegetation. Similar observations of *P. pictus* are lacking, however observational records suggest this species has an affinity with water bodies and possibly preys upon fish, amphibians and lizards (Stuebing et al. 2014, Charlton 2020). Although uncommon, fish predation is observed in some species including garter snakes, e.g. *Thamnophis hammondi* (Kennicott, 1860) (Bell & Haglund 1978), *Agkistrodon piscivorus* (Lacépéde, 1789) (Chiszar et al. 1986), *Eunectes* species (Miranda et al. 2017), Natricidae species (Cundall 1983, Gregory & Isaac 2004) and homalopsine snakes (Voris & Murphy 2002). These aquatic/semi-aquatic species either enter the water body to hunt and capture prey or predate animals adjacent to water sources (Cundall & Greene 2000).

Fishing behaviour involving capturing prey from outside the water body, is seldom observed (Cundall & Greene 2000, Alfaro 2002). This is likely due to the difficulty in detecting prey beneath the water surface and accounting for refraction when striking. Some species counter this difficulty via placing the head on or under the water's surface, relying on fish touching the mouth to initiate a strike (Alfaro 2002, Mario-da-Rosa et al. 2020). Regardless of the difficulties, utilizing aquatic prey can allow numerous similar snakes to utilize the same habitat via the separation of habitat and food resources (Luiselli 2006). Given the morphological similarity of *P. pictus* and *P. pulverulentus*, and their regular documentation within the same habitats (Das 2012, Stuebing et al. 2014, Charlton 2020), some form of separation likely exists between these species. Whether separation occurs at micro-scales (hunting/resting site selection) and/or at macro-scales (habitat selection) is so far unknown due to the paucity of data.

In this study, we use observational data of *P. pictus* and *P. pulverulentus* to determine if separation exists based upon their resting, hunting and ambush site selection (micro-scales) and/or habitat selection (macro-scales). Additionally, we document a successful fishing event in one *P. pictus*, including descriptions of possible fishing behaviour in two other *P. pictus* specimens.

Observations and data for this project were obtained during a long running herpetofauna study (January 2017 to July 2019) within the Deramakot and Tangkulap Forest Reserves in Sabah, Malaysian Borneo (Fig. 1). The reserves comprise hilly, lowland dipterocarp forests (50–350 m a.s.l)

at varying stages of regeneration following logging (reduced impact and conventional selective logging methods). The herpetofauna study comprised 239 days of field work conducted over three years. The study included 59 stream and terrestrial transects (Terrestrial = 12, Stream = 47), surveyed using Standardized Visual Transect Sampling (SVTS: 51 sites, 100 m in length), and Visual Encounter Survey (VES: eight sites, 500 m – 3 km in length) techniques. Transects were surveyed between 3–17 occasions throughout the three years. All surveys were conducted from 1830 hrs to 2330 hrs. During the course of the study we recorded all snakes detected within the SVTS and VES sites. Species identity (distinguished by their distinct dorsal patterning), perch height, distance to water and measurements of the neighbouring water body width and depth, were recorded for all *Psammodynastes* detections. Analysis of *Psammodynastes* habitat data was conducted using unpaired two-sample Wilcoxon tests to determine if significant variation in these covariates exist between species.

We recorded a total of 38 *Psammodynastes* specimens, comprising 21 *P. pictus* and 17 *P. pulverulentus*. The majority of observations occurred in the last year of sampling (n = 24), with the majority of *P. pictus* detected along a single VES stream transect (n = 13). Whilst results of the unpaired two-sample Wilcoxon tests found no significant difference in perch height between species, we found significant dif-

ferences in distance to water (W = 0, p < 0.005), stream width (W = 145, p = 0.008) and stream depth (W = 156, p < 0.005) between both *Psammodynastes* species (Fig. 2). *Psammodynastes pictus* occurred closer to streams (mean: 69.21 ± 48.39 cm) than *P. pulverulentus* (mean: 271 ± 118.13 cm). *Psammodynastes pictus* were associated with wider (mean: 337.05 ± 132.61 cm), deeper streams (mean: 29.62 ± 14.73 cm) compared to *P. pulverulentus,* which were associated with narrower (mean: 174.42 ± 90.85 cm), shallower streams (mean: 10.31 ± 8.8 cm). All *P. pictus* detections occurred within 150 cm of water bodies. In contrast, almost half (n = 7), of all *P. pulverulentus* occurred in terrestrial sites with no adjacent aquatic habitats within 300 m.

On 09/05/2019 at 1854 hrs an adult *P. pictus* (SVL roughly 30–40 cm) was observed perched, over a medium sized river measuring 409 cm wide and 27 cm deep. The snake was perched 15 cm above the water, with the neck coiled in an "S" shape and the head facing the water's surface in the striking position. Within one minute of the observation, the snake struck into the river and subsequently captured a small fish (roughly 4–6 cm long) of the genus *Rasbora*. The snake immediately withdrew the fish from the water, and for the next 5 minutes the fish struggled while the snake held its grip, making no attempt to consume the fish or reposition its jaw (Fig. 3). Following this time, the fish ceased struggling and the snake began manoeuvring
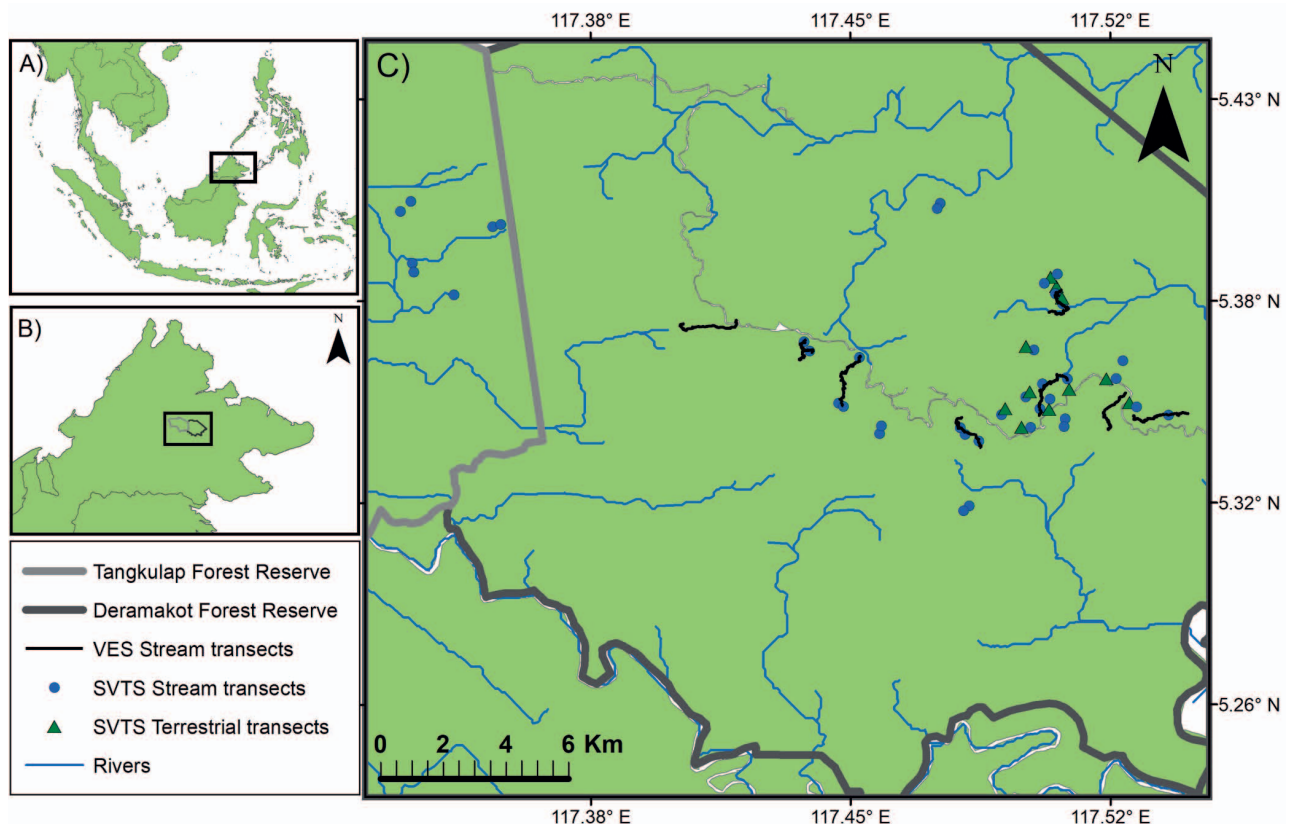

Figure 1. Location of all study transects (VES and SVTS) within the Deramakot and Tangkulap Forest Reserves (C). Location of reserves marked in inset maps (A and B).

its jaws with no assistance from the body, and subsequently began consuming the fish. By 1907 hrs, the snake had completely ingested the fish, and moved back up the branch and adopted a resting position (1 m above the river). We returned to the snake 30 minutes later, where it was still resting in this position.
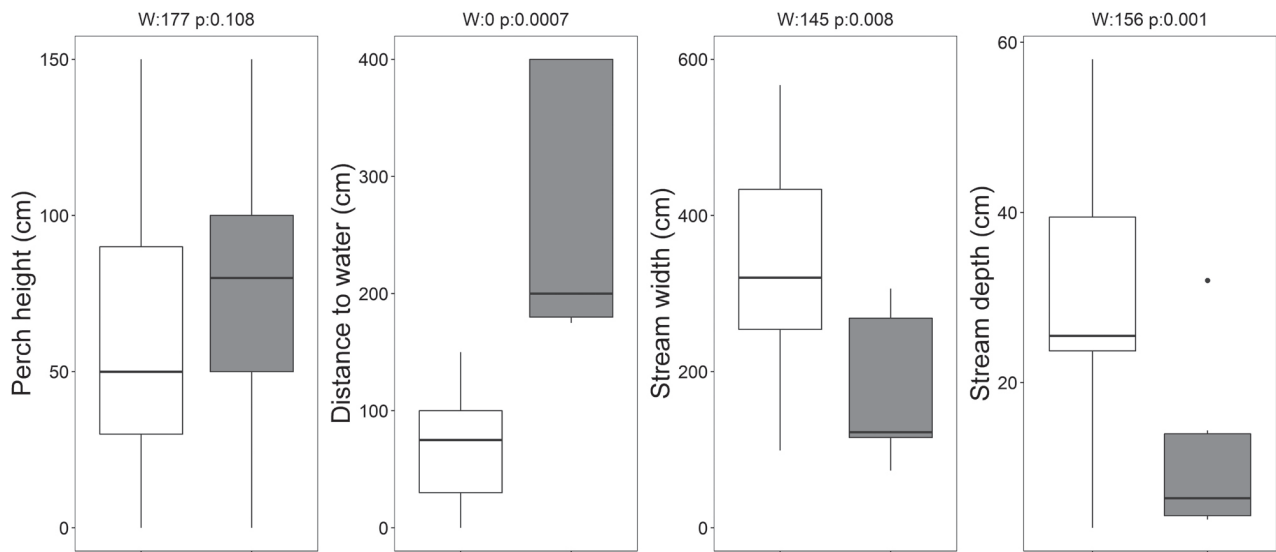

Figure 2. From left to right, values of perch heights, distances to water, and the stream width/depth of adjacent water bodies in *Psammodynastes pictus* (in white) and *P. pulverulentus* (in grey) detections. Results of unpaired two-sample Wilcoxon tests printed above covariate plots.
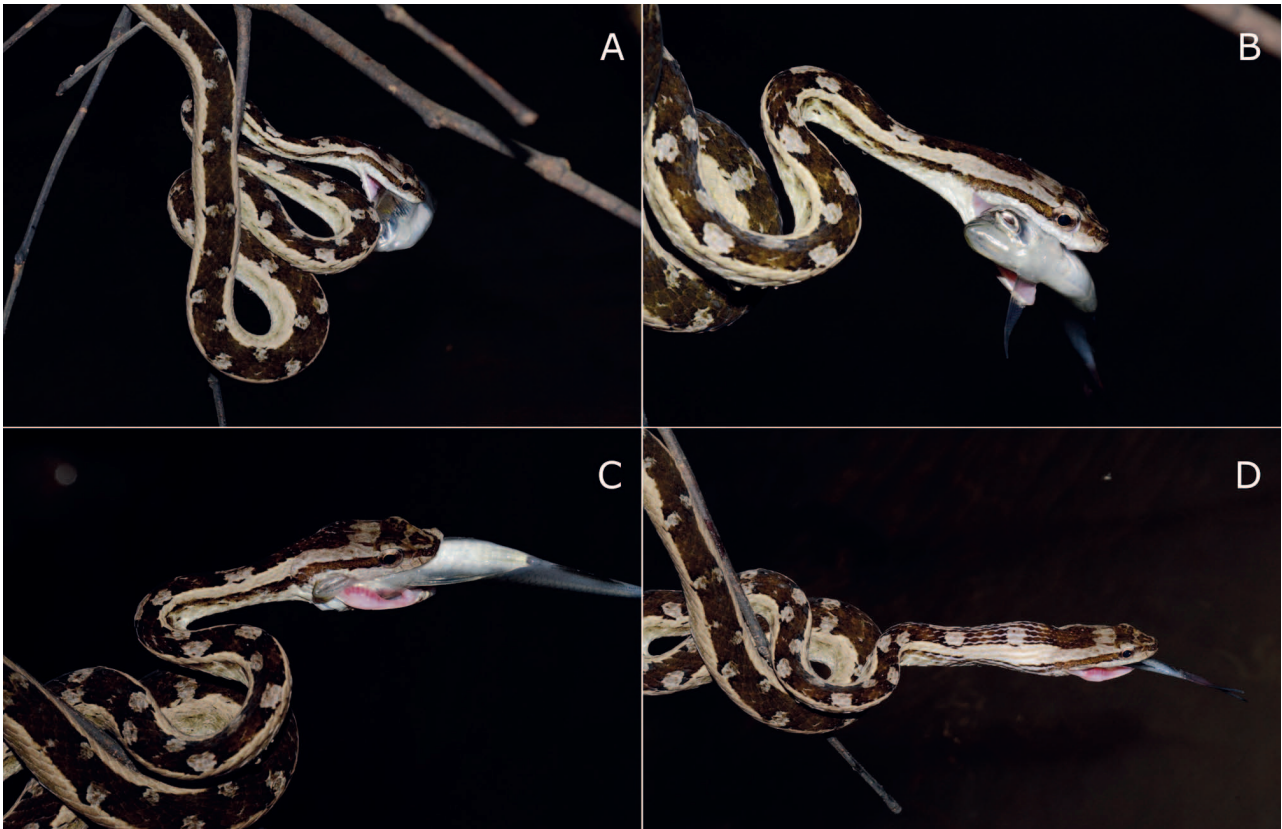

Figure 3. *Psammodynastes pictus* following the capture of a *Rasbora* species, including initial capture (A), repositioning (B and C) and ingestion (D).

Whilst this observation was the only fishing event observed in this species during our study, we observed two other *P. pictus* individuals exhibiting similar behaviour. The other two occasions involved individuals perched on partially submerged fallen tree branches in the middle of the stream (both stream widths between 350–500 cm). The bodies of both snakes were within 10 cm of the water's surface, with heads facing downward in the striking position. However, we observed no successful fish captures or attempts in these two individuals.

When comparing the fishing behaviour of *P. pictus* to other fish-eating snake species, predation strategies appear markedly different. Subaquatic ambushes, with strikes attempted via lateral sweeps of the head instigated via visual detection or prey contact with the mouth form the majority of piscivorous snake hunting strategies (Cundall & Greene 2000, Alfaro 2002). The South American species *Thamnodynastes strigatus* (Günther, 1858) utilizes an arboreal ambush position above the water column. The three successful fishing events recorded from these positions were initiated when fish contacted the mouth placed at the water's surface, with no visual detection or striking from outside the water column observed (Mario-da-Rosa et al. 2020). The *P. pictus* fishing behaviour observed here however, utilized an arboreal ambush site, visual detection and a forward strike from outside the water column. Although only one fishing event and two possible fishing attempts were observed, they represent interesting and novel behavioural observations in this species.

Whilst the results of our habitat separation analysis are based on a limited number of observations (n = 38), they suggest that some macro-habitat separation via distance to adjacent water bodies and stream size exists between the two species. The closer proximity to larger rivers by *P. pictus* could indicate a greater affinity for aquatic habitats compared to *P. pulverulentus*. Furthermore, the documentation of a fishing event in *P. pictus*, and two individuals exhibiting possible fishing behaviour, supports these findings, suggesting a preference for these habitats and their associated resources. This fishing behaviour further explains the apparent preference for proximity to large stream habitats in *P. pictus*. Generally, wider, deeper streams support greater diversity, variable size classes and abundance of freshwater fish (Taylor & Warren 2001, Taylor et al. 2006). These larger waterbodies also support surface feeding niches in fish (Higgins & Strauss 2008), which would put them within striking distance of low hanging *P. pictus*. This abundance and diversity of potential aquatic prey, combined with the fishing behaviour exhibited by this species, could result in the selection of riverine habitats by *P. pictus*. Conversely, whilst our *P. pulverulentus* observations included many away from water, those adjacent to water bodies, were found near small, shallow streams which were also often sloped and rocky. Whilst small, shallow streams often lack high diversity and abundance of fish, we recorded high abundances of small amphibians, including *Leptobrachella parva* Dring, 1984 (SVL 8.5–20 mm), and *Alcalus baluensis* (Boulenger, 1896) (SVL 7–32.5 mm) (Asad et

al. in press), as well as the water skink *Tropidophorus beccarii* Peters, 1871. As *P. pulverulentus* is purportedly a specialist skink predator (Greene 1989), its selection for these streams could be for access to prey items such as *T. beccarii* and/or abundant small amphibians.

Further research and a greater sample size would be needed to verify these observations, however, our results indicate that separation between these species based on distance to water and size of adjacent water body appears to occur. Although causes of any separation can only be theorized, our observation of fishing in *P. pictus*, and this species occurrence close to large rivers, suggests a greater reliance on aquatic habitats and their resources compared to *P. pulverulentus*.

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