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Cover image: *Hippocampus kuda*, Koh Sdach Archipelago (© Roger Bruget). The population trends of this globally Vulnerable species within the archipelago are explored by Kalisiak *et al.* on pp. 47–58 of this volume.

Short Communication

The first record of the Asian bamboo weevil *Cyrtotrachelus rufopectinipes* Chevrolat, 1883 (Coleoptera: Curculionidae: Dryophthorinae) from Cambodia

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The Dryophthorinae Schoenherr, 1825 is one of the few well-defined Curculionidae subfamilies based on morphological and molecular data (Oberprieler *et al*., 2007; McKenna *et al*., 2009; Jordal *et al*., 2014; Shin *et al*., 2018). The group contains five tribes consisting of 153 genera and approximately 1,200 species worldwide (Alonso-Zarazaga & Lyal, 1999; Oberprieler *et al*., 2007; Anderson & Marvaldi, 2014; Chamorro *et al*., 2021). *Cyrtotrachelus*, a genus of Asian bamboo weevils, was established by Schoenherr (1838) and includes more than 22 described species (Heller, 1923). Three are serious pests, namely *C. buquetii* Guerin-Meneville (which includes two subspecies, the nominotypical *C. b. buquetii* and *C. b. borealis* (Jordan)), *C. thompsoni* Alonso-Zarazaga & Lyal (=*C. longimanus* (Fabricius)), and *C. dichrous* Fairmaire (Singh & Bhandari, 1988; Attajarusit, 1996; Wang *et al*., 1998; Alonso-Zarazaga *et al*., 2017; Tseng & Ho, 2019). Other species in the genus include *C. bipartitus* Hartmann, *C. feae* Faust, *C. himalayanus* Heller, *C. lar* Erichson & Burmeister and *C. rufopectinipes* Chevrolat (Singh, 2016; Alonso-Zarazaga *et al*., 2017). Members of the genus are broadly distributed in India, Andaman Island, Nepal, Bangladesh, South China, Taiwan, Japan, Sri Lanka, Sumatra, Java, Malacca, Burma, Borneo, Thailand, Malaysia, Laos, Vietnam, Philippines and Cambodia (Heller, 1923; Morimoto, 1978; Kapur, 1954; Choldumrongkul, 1994; Alonso-Zarazaga & Lyal, 1999; Thapa, 2000; Ju *et al*., 2005; Choudhury *et al*., 2007; Nair, 2007; Hill, 2008; He *et al*., 2009, Panda, 2011; Hogarth, 2013; Singh & Ramesha, 2018). To date, two species, *C. dichrous* Fairmaire, 1878 and *C. thompsoni* Alonso-Zarazaga & Lyal, 1999 have been recorded in Cambodia (Heller, 1923; Morimoto, 1978; Singh & Ramesha, 2018). Alonso-Zarazaga & Lyal (1999) proposed *C. thompsoni* as a replacement name for C. *longimanus* (Fabricius), originally described in *Curculio* Linnaeus, as the latter is a junior homonym (non Forster, 1771). In this article, we present the first record for *C. rufopectinipes* Chevrolat, 1883 in Cambodia.

The biology of *Cyrtotrachelus* spp. is relatively well known due to the economic importance of some of its species. The beetles prefer monocotyledons as host plants, mainly bamboos in India, China, Vietnam and Thailand (Liu *et al*., 1993; Reid, 1995; Chuong *et al*., 2005; Choudhury *et al*., 2007; Shu & Wang, 2015; Patil, 2017; Singh & Ramesha, 2018). An adult female of *C. thompsoni* may lay around 40 elongate eggs (Fu *et al*., 2007). Eggs are placed into oviposition holes made approximately 25 cm from the top of growing bamboo shoots (Singh & Bhandari, 1988; Chuong *et al*., 2005; Wang *et al*., 2005; Panda, 2011). A single bamboo shoot may frequently carry four eggs in different places (Panda, 2011) and a larva emerges from each egg after one or two weeks (Nair, 2007). For approximately four weeks, larvae live inside the host-plant by moving upward (Nair, 2007; Panda, 2011). The last instar larvae burrow into the soil to pupate between 18

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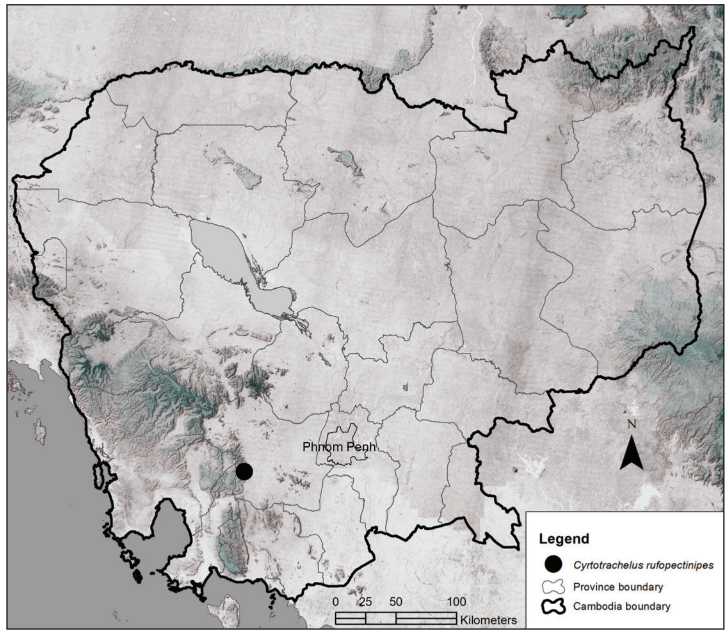

Fig. 1 Location of first record of *Cyrtotrachelus rufopectinipes* Chevrolat, 1883 in Chambok, Kampong Speu Province, Cambodia.

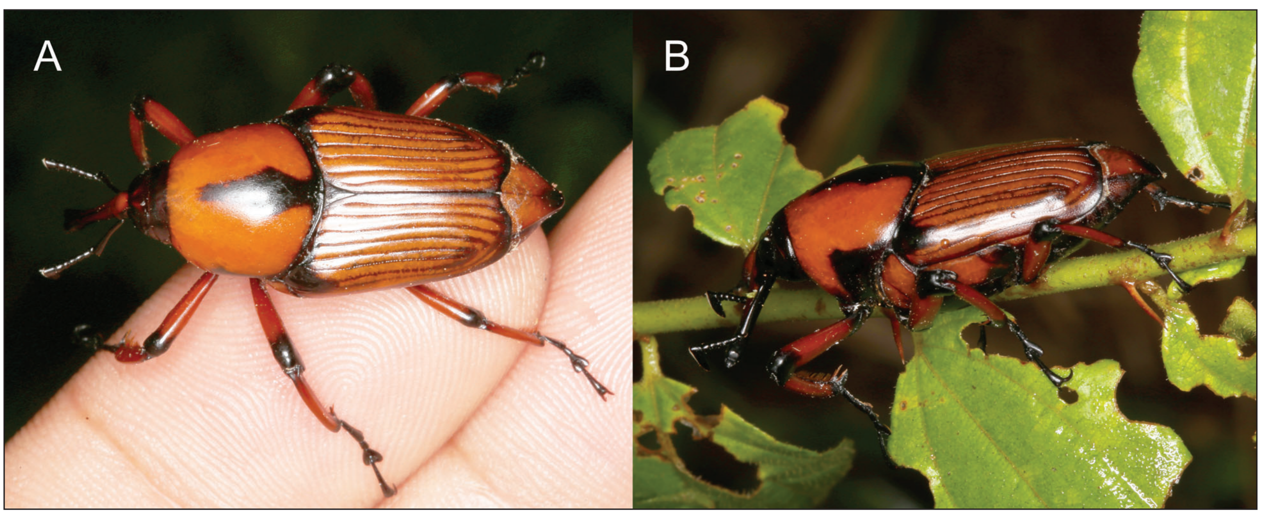

Fig. 2 Live *Cyrtotrachelus rufopectinipes* Chevrolat, 1883 in Chambok, Kampong Speu Province, Cambodia. A) Dorsal view, B) Lateral view (© Phauk Sophany).

to 27 cm deep, with 0.5 to 2.5 m distance from the culms where it remains for three to four weeks (Chuong *et al*., 2005; Patil, 2017). New adults feed on growing shoots of bamboo and after two days of feeding, search for mates (Fu *et al*., 2007). Chuong *et al*., (2005) reported *C. thompsoni* may damage approximately 40% of young shoots in *Dendrocalamus* forest in Vietnam. Moreover, at least 60% of growing shoots of *Bambusa multiplex* were damaged by *C. buquetii* during the wet season in China (Ju *et al*., 2005).

Our record of *C. rufopectinipes* in Cambodia is based on photographs taken during night time sampling of insects by the Cambodian Entomology Initiatives team in Chambok ecotourism site in Kampong Speu Province (Fig. 1). The ecotourism site was established in 2003 and comprises 82.57 km^2 of land which borders Kirirom National Park (Lonn, 2013). Overall, the natural landscape at the site consists of bamboo, degraded semi-evergreen forests and grasslands with deciduous forest (Sin *et al*., 2020; Chhorn *et al*., 2020).

***Cyrtotrachelus rufopectinipes* Chevrolat, 1883** (Fig. 2A-2B)

Cyrtotrachelus birmanicus Faust, 1894; *Cyrtotrachelus montanus* Heller, 1923; *Cyrtotrachelus subnotatus* Voss, 1931

Diagnosis: This species is characterized by a red pronotum with longitudinal black vittae exceeding the median region. The elytra are red with striae I-V strongly punctate compared to striae VII-X (Fig. 2A). The front leg is shorter than body length. As we did not collect a voucher specimen, our identification is based on photographs and observations made in the field which agree with the identification key provided by Tseng & Ho (2019).

Distribution: Cyrtotrachelus rufopectinipes is widely distributed in China, northeast India (Sikkim & Assam), Sri Lanka, Java, Nias, Burma, and Vietnam (Tonkin) (Heller, 1923; Singh & Ramesha, 2018). Our observation constitutes the first record of the species in Cambodia.

Record locality: We observed and photographed the species on 18 October 2019 on a trail in bamboo forest (11°22′41.14″N, 104°6′50.85″E, 110 m a.s.l) within the Chambok ecotourism site, Phnom Srouch District, Kampong Speu Province.

Including our record, three species of *Cyrtotrachelus* are now documented in Cambodia. Bamboo forests account for around 0.33% (35,802 ha) of forests in the country (FA, 2007) and play a significant role in contributing to the subsistence livelihoods of rural people and providing natural habitat for biodiversity (Mouy, 2010). However, interactions between *Cyrtotrachelus* species and bamboo have not been documented in the country, nor have the potential damage caused by some of these species. *Cyrtotrachelus* species include several serious pests of bamboo in Southeast Asia (Tseng & Ho, 2019) and it would be interesting to learn more about their biology and distribution in the region. Investigations are needed to determine the potential impact, if any, these species have on native bamboo stands in Cambodia.

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Irrawaddy dolphin *Orcaella brevirostris* strandings between 2017 and 2020 in Kep Province, Cambodia

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ប្រជុំកោះកែបនៃប្រទេសកម្ពុជា ទ្រទ្រង់ដល់ប្រភេទសត្វប្លែកៗមួយចំនួន ដែលដើរតួយ៉ាងសំខាន់ក្នុងប្រព័ន្ធអេកូឡូស៊ី ដោយរួមមានសត្វផ្សោតក្បាលត្រឡោក (*Orcaella brevirostris*) ផងដែរ។ ប៉ុន្តែពុយឡាស្យុងផ្សោតក្បាលត្រឡោកនេះ កំពុងមានការចាប់អារម្មណ៍សិក្សាស្រាវជ្រាវកាន់តែច្រើនឡើង ខណៈពេលដែលពួកវាកំពុងទទួលរងនូវការគំរាមកំហែងកាន់តែច្រើនឡើងពីសកម្មភាព មនុស្សដូចជា៖ ការបំពុល និងការនេសាទខុសច្បាប់ គ្មានការរាយការណ៍ និងការគ្រប់គ្រង។ ការសិក្សានេះ រាយការណ៍ពីការងាប់របស់សត្វផ្សោតក្បាលត្រឡោកចំនួន១០ក្បាលក្នុងខេត្តកែប ក្នុងអំឡុងឆ្នាំ២០១៧ ដល់ ២០២០ និងកំណត់ត្រាអំពីរបួសទាំងខាងក្រៅ និងខាងក្នុងខ្លួន ដោយការវះកាត់សាកសពផ្សោតនីមួយៗ ក៏ដូចជារបាយរដូវ និងប្រជាសាស្ត្រនៃព្រឹត្តិការណ៍កឿងងាប់នីមួយៗ។ ការកឿងងាប់កើតឡើងនៅទូទាំងប្រជុំកោះ និងគ្រប់រដូវ ប៉ុន្តែប្រទះឃើញច្រើននៅចុងរដូវវស្សា (ពីខែតុលា ដល់ វិច្ឆិកា)។ ផ្សោតមិនទាន់ពេញវ័យងាយនឹងកឿងងាប់ជាង ប៉ុន្តែគេមិនបានប្រទះឃើញមានកូនផ្សោតងាប់ទេ។ គេមិនទាន់អាចកំណត់ពីមូលហេតុជាក់លាក់នៃការងាប់របស់ពួកវានៅឡើយទេ ដោយសារកង្វះខាតធនធាន និងបុគ្គលិកជំនាញ។ ទោះជាយ៉ាងណា គេយល់ថា ការងាប់គឺបណ្តាលមកពីជំងឺ សារធាតុគីមីពុល និងការនេសាទបានដោយចៃដន្យ។ ការសង្កេតពីអាហារក្នុងក្រពះ បានបញ្ជាក់ថា ត្រីឆ្អឹងតូចៗ សប្បិសត្វ និងពពួកមឹកគឺជាចំណីរបស់ពួកវា។ ជាអនុសាសន៍ យើងសុំស្នើឲ្យបន្តការតាមដានពីការកឿងងាប់របស់សត្វផ្សោតក្បាលត្រឡោកនៅតាមតំបន់ឆ្នេរនៃប្រទេសកម្ពុជា រួមជាមួយនឹងគំនិតផ្តើមបង្កើតបណ្តាញត្រួតពិនិត្យការងាប់ផ្សោតតាមតំបន់ឆ្នេរ ដែលមានការគាំទ្រគ្រប់គ្រាន់ខាងផ្នែកថវិកា ធនធាន សម្ភារៈ និងការបណ្តុះបណ្តាលអ្នកជំនាញ ដូចជាផ្នែកពេទ្យថនិកសត្វសមុទ្រជាដើម។ ព័ត៌មានដែលប្រមូលបានពីបណ្តាញខាងលើ អាចនឹងជួយបង្កើនការយល់ដឹងផ្នែកកាយវិភាគវិទ្យា សរីរៈវិទ្យា និងរោគវិទ្យានៃផ្សោតក្បាលត្រឡោក ហើយវាក៏ជាព័ត៌មានសម្រាប់ការរៀបចំយុទ្ធសាស្ត្រអភិរក្ស និងគ្រប់គ្រងប្រភេទនេះ។

Abstract

The Kep Archipelago in Cambodia supports a variety of ecologically important species, including the Endangered coastal Irrawaddy dolphin *Orcaella brevirostris*. This dolphin population has recently been subject to increased research, but faces growing threats from a variety of anthropogenic pressures, including pollution and illegal, unreported and unregulated fishing activity. This study reports on the fatal strandings of ten Irrawaddy dolphins in Kep Province between 2017 and 2020 and documents the internal and external injuries recorded during rudimentary necropsies as well as the distribution, seasonality and demography of the stranding events. The strandings occurred throughout the archipelago in all seasons, although they were most prevalent during the post-monsoon season (October to November). Juveniles were most susceptible to stranding and no strandings of calves were recorded. The causes of death could not be accurately determined due to a lack of resources and trained personnel, although disease, chemical pollution and

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bycatch would appear to be the most likely causes of stranding. Observations of stomach contents confirmed small bony fish, crustaceans and cephalopods as prey species. We recommend continual monitoring of Irrawaddy dolphin strandings along the Cambodian coastline, with a view to establishing a coastal-wide stranding network supported by adequate funding, resources, facilities and trained personnel such as marine mammal veterinarians. The information gathered from such a network would enhance understanding of the anatomy, physiology and pathology of Irrawaddy dolphins and inform conservation and management strategies for the species.

Keywords Cambodia, diet, distribution, Indo-Pacific, Irrawaddy dolphins, IUU fishing, necropsy, seasonality, strandings, stranding networks.

Introduction

Irrawaddy dolphins *Orcaella brevirostris* are an endangered, euryhaline species with a declining population and a discontinuous distribution across the Indo-Pacific coastline (Stacey & Arnold, 1999; Minton *et al*., 2017; Smith, 2018; Kumar *et al*., 2019). Irrawaddy dolphins are uniformly dark grey on the dorsal and lateral fields, with a lighter ventral field (Smith, 2018). Body lengths of sexually mature individuals are 2.1–2.2 m for females and as large as 2.8 m for males (Smith, 2018). The diet of the species consists of small bony fish, cephalopods and crustaceans (Baird & Mounsouphom, 1997; Ponnampalam *et al*., 2013; Jackson-Ricketts *et al*., 2018). Irrawaddy dolphins are currently categorised as Endangered by the IUCN Red List (Minton *et al*., 2017). However, five subpopulations have been reported as 'Critically Endangered' (Malampaya Sound, Philippines; Chilika Lagoon, India; Ayeyarwady River, Myanmar; Mahakam River, Indonesia; Songkla Lake, Thailand; Mekong River, Cambodia, Laos and Vietnam; Smith, 2007; Minton *et al*., 2017). The main natural predators of Irrawaddy dolphins are believed to be sharks (Khan *et al*., 2011). However, key threats to the species are of anthropogenic origin and include entanglement in fishing gears, habitat loss and fragmentation, pollution (industrial and noise), and live capture for aquaria (Nelson, 1999; Smith, 2007; Smith *et al*., 2008; Smith, 2009; Minton *et al*., 2017). The first major documented decline of Irrawaddy dolphins in Cambodia occurred during the Pol Pot regime (1975 to 1979) when dolphins were shot by Vietnamese soldiers for target practice. Dolphin oil was used by the Khmer Rouge for lamps, motorbikes and boat engines, and their meat was consumed as food (Tana, 1995; Perrin *et al*., 1996; Baird & Beasley, 2005; Beasley 2007; Beasley *et al*., 2013). Since the early 2000's Irrawaddy dolphins have become a flagship species for the conservation of marine and freshwater ecosystems in Cambodia (Beasley, 2007; Deutsch, 2020), and they are now protected from targeted hunting by national and international regulations (Minton *et al*., 2017; Ministry of Agriculture, Forestry and Fisheries [MAFF], 2018). Despite these measures, Irrawaddy dolphin strandings and bycatch events occur regularly in Cambodia and across their range (Smith, 2007; Dove, 2009; Kumar *et al*., 2019; Tubbs *et al*., 2019; Kreb *et al*., 2020).

Nine cetacean species have been observed in Cambodian waters: false killer whale *Pseudorca crassidens*, Indo-Pacific bottlenose dolphin *Tursiops aduncus*, Indo-Pacific common dolphin *Delphinus tropicalis*, Indo-Pacific finless porpoise *Neophocaena phocaanoides*, Indo-Pacific humpback dolphin *Sousa chinensis*, Irrawaddy dolphin, pantropical spotted dolphin *Stenella attenuata*, short-finned pilot whale *Globicephala macrohynchus* and spinner dolphin *S. longirostris* (Beasley & Davidson, 2007). Whilst sightings and strandings of these species have been recorded along the Cambodian coastline, only two marine mammal species have been observed within the Kep Archipelago, Irrawaddy dolphins and dugongs *Dugong dugon*. Two peer-reviewed papers have described strandings of Cambodia's coastal Irrawaddy dolphins to date (Tubbs *et al*., 2019; Jones *et al*., 2021). This paper aims to build on this knowledge base and contribute to conservation and management through improved implementation of Cambodia's marine mammal stranding network.

Beasley & Davidson (2007), Bohm (2019), Tubbs *et al*. (2019) and Hines *et al*. (2020) highlighted threats posed by illegal, unregulated and unreported (IUU) fishing activity to marine mammals (notably Irrawaddy dolphins and dugongs), including bycatch, habitat degradation, and prey depletion. Cambodian fisheries law prohibits the use of electrified gears, gillnets and seine nets with a mesh size smaller than 1.5 cm, pair trawling nets, and bottom trawling at a depth less than 20 m (MAFF, 2007). Despite these laws and attempted enforcement, IUU fishing, including the use of electrified nets, small-mesh gill and seine nets, and shallow water bottom-trawling, continues to be observed across the Cambodian coastline (Nelson, 1999; Beasley & Davidson, 2007). For instance, non-compliance to fisheries law frequently occurs within the Kep Archipelago including daily observations of both Cambodian and transnational vessels bottom-trawling, electric trawling and pair-trawling (Bohm, 2019; Tubbs *et al*., 2019). This illegal activity results in marine mammal entanglement, bycatch and habitat degradation (Nelson, 1999; Beasley & Davidson, 2007; Minton *et al*., 2017; Tubbs *et al*., 2019, 2020).

The frequent non-compliance with fisheries law is due to the complex socio-political and economic challenges facing a developing country such as Cambodia. Lack of funding and other resources make it difficult to enforce and issue appropriate sanctions for IUU fishing at the local and transnational level (Bohm, 2019) and limits capacity for compensating compliant actors and conservation efforts within constituent fishing communities. Similar parallels can be drawn between the Critically Endangered vaquita *Phocoena sinus* in the Sea of Cortez and the ongoing threat from IUU fishing targeting *Totoaba macdonaldi* (Jaramillo-Legorreto *et al*., 2016; Cisneros-Mata *et al*., 2021). Current conservation actions in Cambodia include in-situ research and monitoring of identified Irrawaddy dolphin populations, establishment of protected areas, and inclusion of the species in international legislation including the Convention on International Trade in Endangered Species (Appendix I) and the Convention of Migratory Species (Smith, 2007; Minton *et al*., 2017). Although studies have highlighted the need for further research and habitat and species-specific conservation strategies (Tubbs *et al*., 2019; Jones *et al*., 2021), coordination of an effective and well-resourced stranding network is integral to improving understanding of Irrawaddy dolphins, reliably identifying the causes of strandings and reducing the likelihood of these where possible.

The Cambodian Marine Mammal Conservation Project (CMMCP) was established by the non-government organisation Marine Conservation Cambodia in 2017 and combines scientific research and monitoring with protected area management and national government collaboration. These efforts are focussed in the Kep Archipelago which supports a small resident population of coastal Irrawaddy dolphins (Tubbs *et al*., 2019, 2020). The archipelago was recognised as a Marine Fisheries Management Area (MFMA; equivalent to a marine protected area: Reid *et al*., 2019) in 2018 and later, as an Important Marine Mammal Area (MMPATF, 2019). This study presents data collected by the CMMCP on fatal strandings of Irrawaddy dolphins in the Kep Archipelago between November 2017 and November 2020 (including those reported by Tubbs *et al*., 2019 and Jones *et al*., 2021). Sex and age class were investigated independently, while the distribution of stranding sites and seasonality of stranding events were compared with the population distribution and seasonality data reported by Tubbs *et al*. (2020). The aim of this research is to instigate and inform a coastal-wide marine mammal stranding programme for Cambodia, with the potential for collecting valuable data regarding Irrawaddy dolphin biotoxins, contaminants, cytology, genetics, histology, life history, microbiology, parasitology and virology, as well as identifying and confirming threats facing the species along the country's coastline. This knowledge, along with lessons learnt from other strandings programs within the Indo-Pacific region, can be used to inform and guide a national marine mammal strandings response, to ensure effective species conservation and habitat management at local, national and transnational scales.

Methods

Study area

Cambodia's coastline extends 17,791 km^2 (Rizvi & Singer, 2001) and includes four coastal provinces: Koh Kong (10,090 km^2), Sihanoukville (2,536 km^2), Kampot (4,873 km^2) and Kep (335 km^2). Cambodia's neritic zone features a number of closely interrelated ecosystems, beaches, forests, mangroves, estuaries, seagrass beds and coral reefs with a gently sloping, relatively shallow seabed (Rizvi & Singer, 2011). Kep, Cambodia's smallest coastal province, is home to an archipelago of 13 islands extending approximately 15 km offshore. The Kep Archipelago (Fig. 1B) is a shallow (≤ 12 m depth), coastal region with two riverine inputs, the Giang river to the east and the Kampot river to the northwest. The archipelago includes important marine ecosystems including seagrass meadows, coral reefs and mangrove forests, which provide habitats for endangered fauna including Irrawaddy dolphins, green sea turtles *Chelonia mydas* and hawksbill sea turtles *Eretmochelys imbricata*, dugongs and seahorses *Hippocampus* spp. (Beasley & Davidson, 2007; Reid *et al*., 2019; Tubbs *et al*., 2019; Strong *et al*., 2021). Formally designated in 2018 as an MFMA, the region protects 113 km^2 of archipelagic waters which provide a potential refuge for Kep's resident population of Irrawaddy dolphins (Tubbs *et al*., 2019, 2020). The archipelago is bordered on three sides by Vietnam (Fig. 1A) and as a result attracts transnational IUU fishing activity in the form of bottom trawling and electric trawling from both Cambodian and Vietnamese vessels (Bohm, 2019; Strong *et al*., 2021). Only small-scale sustainable subsistence fishing activities such as pot fishing and hook-and-line fishing are permitted within the fisheries protected areas (which represent 100 km^2 of Kep MFMA), while all fishing activity is prohibited within the conservation, and research and recreation areas (5.2 km^2). For the duration of this study, the research team inhabited Koh Ach Seh, an island located within a conservation zone approximately 13 km from mainland Kep (Fig. 1B).

Recovery and necropsy of carcasses

Irrawaddy dolphin carcasses were recovered by the CMMCP between November 2017 and November 2020. Strandings within the archipelago and along the Kep coastline were reported to the CMMCP by local fishers and community leaders or discovered by the CMMCP research team during routine surveys and patrols of Koh Ach Seh and the Kep Archipelago. Once the locations of individual strandings were confirmed, GPS coordinates were recorded using a Garmin 64s GPS unit and a carcass recovery procedure was initiated.

Carcasses found on land were photographed and transported on foot using a tarpaulin sheet to a safe location away from the shoreline. Where appropriate, a basic on-site necropsy was conducted. Body measurements and photographs were taken along with teeth, bone and tissue samples for future laboratory analysis. Sex was determined by external and internal examination of sex organs, and the age class of each individual was categorized as adult (> 2.2 m length), juvenile (1.30–2.19 m length) or calf (< 1.3 m length) based on body measurements and confirmed by other indicative factors such as odontogeneses. A rudimentary investigation of internal organs and tissues was undertaken to assess the internal body condition of each individual and helped to determine factors which may have contributed to death, such as plastic ingestion. Internal and external assessments, environmental factors and confirmed regional threats were used to ascertain the suspected cause of stranding. Carcasses were buried 1–1.2 m deep on Koh Ach Seh and the coordinates of each burial site were recorded. Some carcasses were later exhumed to collect additional samples such as bone after the initial phase of tissue decomposition.

On discovering a carcass in water, photographs were taken and the site coordinates were collected using a Garmin 64s GPS. Recovery of these carcasses was dependent on the distance of the site from the research island of Koh Ach Seh. For instance, as one of the carcasses was sighted < 300 m from the island, two individuals waded out to retrieve the carcass using a tarpaulin sheet. The second carcass in water was discovered ca. 3 km east of Koh Tbal during a routine boat-based survey (Fig. 2A; Jones *et al.*, 2021). In this case, the research vessel was used to approach and tow the carcass back to Koh Ach Seh. The carcass was secured to the stern of the vessel by the tail fluke using a 5 m length of rope and the vessel maintained a speed of 7.4 km/hr to avoid damaging or deforming the carcass prior to examination. Once recovered to a safe location, the same measurements, assessments and burial procedures were conducted as above.

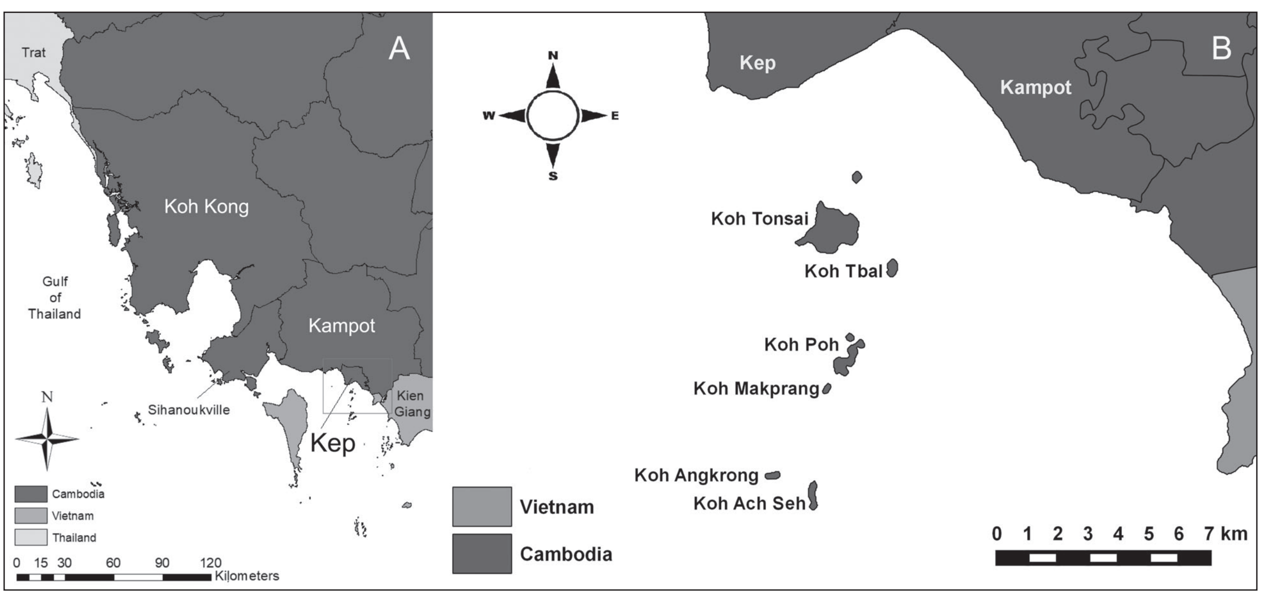

Fig. 1 A) Eastern Gulf of Thailand highlighting the Kep Archipelago (outlined area), B) The Kep Archipelago, including Koh Ach Seh where the research team resided during the study.

Distribution of strandings

The distribution of strandings was mapped using QGIS (ver. 2.8.5). The GPS locations for each Irrawaddy dolphin carcass were uploaded as point data and used to create a raster heatmap highlighting stranding hotspots. Each point was given a heat radius of 1 km and was proportioned as the number of strandings (count data) with a mean standard deviation of 2.0. Colour interpolation was set as linear with a single-band pseudo-colour render type.

Seasonality of stranding events

We report the seasonality of Irrawaddy dolphin stranding events as the mean number of stranding events per month and per season over the three-year study period. Seasons were categorised as pre-monsoon (March to April), summer monsoon (May to September), post-monsoon (October to November) and dry (December to February), as defined by Tsujimoto *et al*. (2018). Due to our small sample size (n = 10), we employed a one-tailed Fisher's exact test of independence (FET) rather than a Chi-squared (X^2) test (Winters *et al*., 2010) to investigate differences in stranding events across seasons. The influence of sex and seasonality on strandings was also assessed, although not statistically due to the small sample size.

Results

Distribution of strandings

Irrawaddy dolphin carcasses were recovered throughout the Kep Archipelago and within the Kep MFMA (Figs. 2A–2B). Eight carcasses were encountered on land (comprising four reported to CMMCP and four discovered by the research team) and two in water (Fig. 2A). The waters around Koh Ach Seh were the primary hotspot for strandings, accounting for 40% of all strandings recorded (Fig. 2B). A secondary hotspot was located in the northern archipelago along the southern tip of the Kep mainland, which accounted for 30% of the recorded strandings. The remaining 30% occurred in a trilateral formation between Koh Tonsai, Koh Poh and the waters to the east of Koh Tbal.

Seasonality of stranding events

Stranding events occurred in all seasons with a mean of 2.5 strandings per season during the study period (Fig. 3). The number of stranding events observed per season differed significantly (FET, p = 0.0215), indicating that these were not seasonally uniform. Stranding events were most prevalent during the post-monsoon season with four occurring in October and November during the study period (Fig. 3). In contrast, stranding events were least prevalent during the summer monsoon season (May to September), with just one stranding event. The post-monsoon season consequently accounted for 40% of all stranding events, whereas the remaining three seasons accounted for 60%.

Although stranding events occurred in all seasons, male and female strandings only co-occurred during the post-monsoon and dry seasons (Fig. 4). Male strandings were most prevalent during the pre-monsoon season (n = 2) when no female strandings were recorded. In contrast, no male strandings were recorded during the summer monsoon season, when one female stranding occurred. Female strandings were most prevalent during the post-monsoon season (n = 2) and an equal proportion of male and female strandings occurred during the dry season.

Our measurements of body length identified four adults and four juveniles. Strandings of calves were not observed during the study. Adult strandings occurred during three of the four seasons, pre-monsoon, post-monsoon and dry, whereas juvenile strandings occurred in all seasons (Fig. 5). Adult strandings were most prevalent during the post-monsoon season (n = 2), whereas juvenile strandings were equally prevalent in all seasons (n = 1 /season).

Necropsy findings: Sex, age, body measurements and suspected cause of strandings

Sex and age class was confirmed through necropsy of eight of the ten stranded individuals included in our study. The remaining two individuals were not examined due to the difficulty of carcass recovery and transport. For the eight individuals necropsied, four were identified as male and four as female. According to the Decomposition Condition Code (DCC) outlined by Pugliares *et al*. (2007), one female carcass was considered fresh with a DCC of 2. Six carcasses, comprising four males and two females, were in a state of moderate decomposition with a DCC of 3, and the remaining female carcass was found in a state of advanced decomposition with a DCC of 4. Tissue, teeth and bone samples were taken from all necropsied individuals. Examinations of body size and odontology identified four of the carcasses as adults and four as juveniles. The adults consisted of three males and one female, whereas the juveniles consisted of three females and one male.

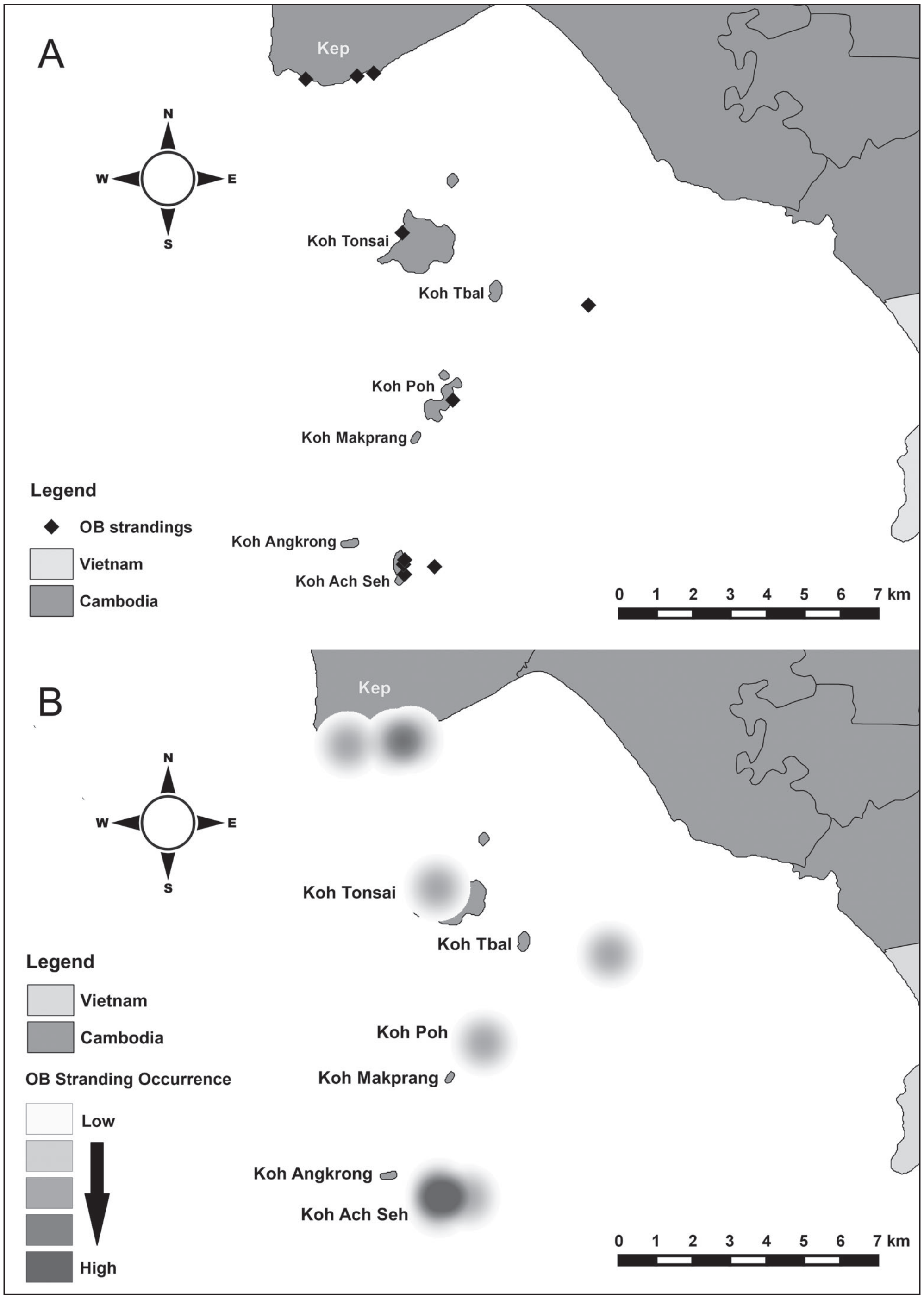

Fig. 2 Distribution of A) Irrawaddy dolphin stranding events (OB) in the Kep Archipelago and on the Kep mainland between 2017–2020, B) Hotspots of Irrawaddy dolphin stranding events during the same period.

Future analysis of samples from carcasses with DCC values of 2 and 3 may provide information about histology, virology, parasitology, contaminants, biotoxins, life history and genetics, whereas analysis of DCC 4 samples may only provide information about histology, virology, life history and genetics (Pugliares *et al*., 2007). The cause of deaths of all individuals remains uncertain due to the lack of trained personnel, levels of decomposition observed and ambiguities regarding whether external injuries occurred before or after death.

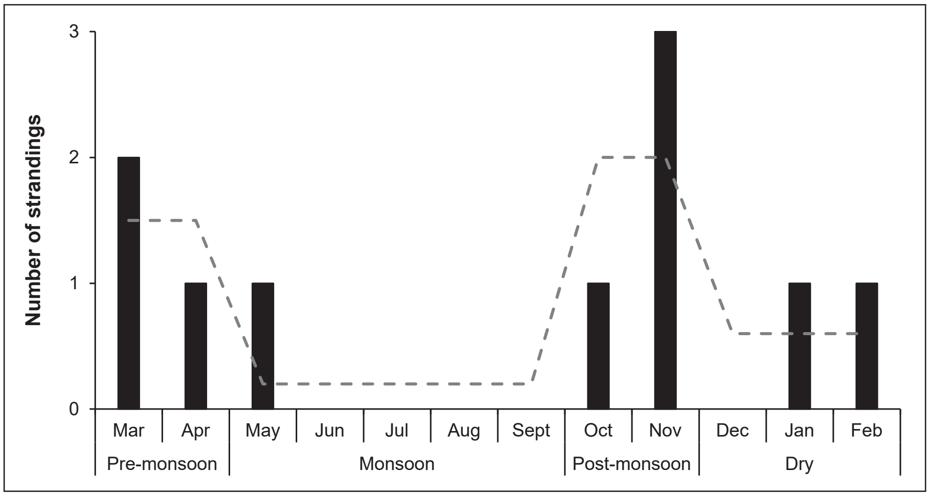

Fig. 3 Seasonality of Irrawaddy dolphin stranding events in the Kep Archipelago between 2017–2020. The dashed line indicates the mean number of strandings per season over the three-year study period.

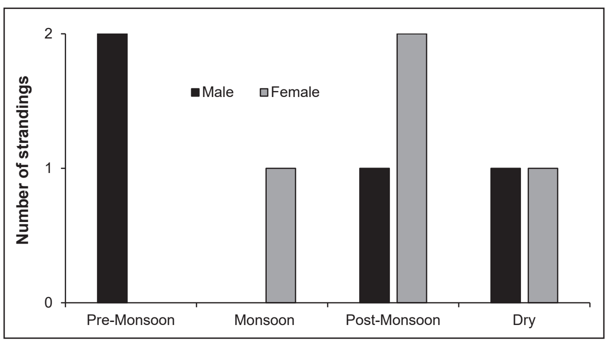

Fig. 4 Seasonality of male and female Irrawaddy dolphin strandings within the Kep Archipelago between 2017–2020.

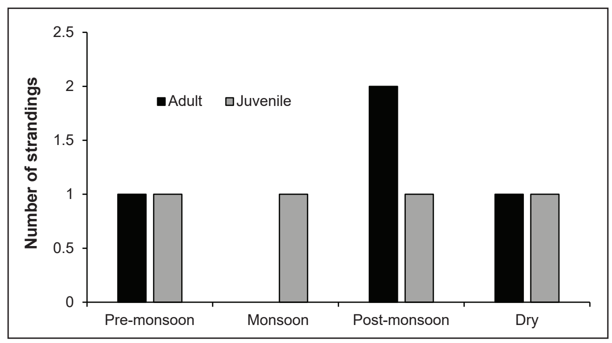

Fig. 5 Seasonality of adult and juvenile Irrawaddy dolphin strandings within the Kep Archipelago between 2017–2020.

However, our study does identify regional threats including IUU fishing activity, habitat degradation, prey depletion, chemical pollutants and historical hunting as contributing stressors likely to impact Irrawaddy dolphin health (individual and population).

Despite external examinations of the stranded individuals, we could not accurately determine cause of death due to carcass decomposition and uncertainties regarding primary and secondary injuries and diseases. Five carcasses showed evidence of interactions with fishing gear, such as the tail fluke enmeshed in netting and rope. In one case, the tail fluke of a stranded individual had been completely severed (Figs. 7A–7B) and possible causes include primary and secondary predation by sharks, or interaction with boats (e.g., propellers) and fisheries. There was no evidence of starvation or emaciation based on external examination.

Basic internal examinations indicated that all individuals had healthy stomach contents, with no evidence of plastic ingestion. Stomach contents included small fish bones including otoliths, squid beaks and shrimp tails (Figs. 6A–6B), confirming these as prey species for Kep's population of Irrawaddy dolphins. Fish bones were thought to be those of *Cirrihinus siamensis* and *Paralaubuca typus* (Baird *et al*., 1994). Stable isotope analyses were not conducted on stomach contents.

While the exact cause of death could not be confirmed, our findings suggest the following as possible causes of death: bycatch, chemical pollution, disease and other natural causes including predation. Disease and bioaccumulation of toxins within systems is highly likely to impact survival, leaving the afflicted individual more susceptible to bycatch or stranding.

Fig. 6 Stomach contents of Irrawaddy dolphins stranded in the Kep Archipelago between 2017–2020. A) Small bony fish, undigested fish bones and squid beaks, B) Small bony fish and shrimp tail.

Fig. 7 Irrawaddy dolphins stranded in the Kep Archipelago. A) Adult male with a severed tail fluke on Koh Poh, B) Stranded individual with severed tail fluke, C) Juvenile female with burns and protruding organs on Koh Ach Seh, D) Adult male with severe blistering and flesh wounds, E) Collection of tissue, bone and teeth samples from a juvenile female on Koh Ach Seh, F) Stomach contents of an adult female found at sea west of Koh Tbal.

Discussion

Most of the strandings in this study occurred close to land, with a primary hotspot around Koh Ach Seh where four of the ten strandings were discovered. A secondary hotspot (three strandings) was located in the north of the archipelago along the southern tip of the Kep mainland. Stranding events occurred in all seasons but were most prevalent during the post-monsoon season (October to November) and least prevalent during the summer monsoon season (May to September). Necropsy findings showed evidence of external injuries typical of intra and/or interspecific interactions, including but not limited to humans, sharks and other Irrawaddy dolphins. Sex was not a determining factor in stranding likelihood, although with 50% of the identified individuals being juveniles (an unrepresentative proportion of the population), juveniles would appear to be substantially more vulnerable to stranding. Finally, while yearly trends showed a small decline in strandings events over time, from four in Year 1 to three apiece in Years 2 and 3, this plateaued with recorded strandings remaining at three per year.

Distribution, seasonality, sex and age

Our data on Irrawaddy dolphin stranding events in the Kep archipelago directly overlaps with the sightings and strandings data reported by Tubbs & Croxford (2019) and Tubbs *et al*. (2020), where dolphin sightings were clustered around Koh Ach Seh and the central archipelagic islands. This overlap highlights the Kep Archipelago as a critical yet threatened habitat for Irrawaddy dolphins. Our data also notably overlaps with reported IUU fishing activity within the region (Bohm, 2019), with strandings distributed in areas with regular and concentrated IUU fishing activity, specifically bottom trawling and electric trawling (Bohm, 2019), further emphasising the likelihood of bycatch as cause of death.

Observer bias almost certainly accounts for the higher number of strandings recorded around Koh Ach Seh, as their discovery was more likely due to the continuous presence of the research team. Similarly, observer bias may have led to a greater number of stranding reports around the Kep mainland as it is more densely populated than the archipelagic islands. To reduce this bias, a small-scale marine mammal stranding network was established in collaboration with local communities in November 2017 to facilitate reporting from the less densely populated islands of Koh Poh and Koh Tonsai.

The spatial distribution of strandings reported may also be explained by seasonal shifts in the prevailing winds. For example, the northeast prevailing winds occurring during the dry (December to February) and pre-monsoon seasons (March to April) may explain the seasonal increase in strandings on mainland (north) and western shorelines such as at Koh Tonsai. Conversely, southwest prevailing winds during the summer monsoon and post-monsoon seasons (May to November) may explain the prevalence of strandings in the east of the archipelago during the post-monsoon season such as those discovered at Koh Ach Seh and Koh Poh.

Stranding events were most prevalent during the post-monsoon season (40%), despite this only accounting for two months of the year. Tubbs *et al*. (2020) reported highest encounter rates for Irrawaddy dolphins in the archipelago during this season and attributed this to freshwater inputs and variations in prey distribution. As greater numbers of dolphins congregate in this area at this time, they are more vulnerable to threats including overfishing, bycatch and pollution. In addition, the post-monsoon season is characterised by high winds and storm events which make it difficult for law enforcement and fisheries officers to patrol the region, and this in turn results in more IUU fishing activity (Bohm, 2019; Thap R., unpublished data), increasing the threat and likelihood of dolphin strandings.

Cultural celebrations may also explain the seasonal increase in IUU activity. The water festival (*Bon Om Thook* in Khmer), a traditional Southeast Asian celebration, typically occurs in late October to early November and is celebrated with a fluvial parade and seafood banquets. This seasonal increase in seafood demand leads to a localised surge in IUU fishing activity within the Kep Archipelago, particularly bottom trawling, by both Cambodian and Vietnamese vessels (Thap R., unpublished data), resulting in increased habitat degradation and likelihood of dolphin strandings.

Our analysis of age and seasonality did not reveal any calf strandings during the study period. Conversely, juvenile strandings occurred during all seasons, whereas adult strandings did not, suggesting that juveniles are more vulnerable to stranding throughout the year. Despite accounting for 24% of sightings on average (calculated from land and boat-based sightings between 2017 and 2020: Tubbs *et al*., 2020), juveniles also accounted for 50% of strandings in the Kep Archipelago during our study, indicating that they are disproportionately susceptible to stranding and premature death. Other studies found similar results in wild Irrawaddy dolphin populations, attributing premature death in juveniles to disease (*Aeromonas hydrophila* and other opportunistic bacterial diseases: Dove, 2009), environmental contaminants (DDT, PCBs and mercury: Dove, 2009), inbreeding depression (Dove, 2009; Krutzen *et al*., 2018) and interactions with fisheries (Reeves *et al*., 2009). Juvenile stranding events pose a significant concern for the long-term survival of Irrawaddy dolphin populations. Low genetic diversity, fragmented populations and slow reproduction rates, coupled with increasing population extirpations and mounting anthropogenic pressures, highlight the urgent need for improved species and habitat protection. Interactions with fisheries have been emphasized as the primary threat to Irrawaddy dolphins in both the Mekong (Reeves *et al*., 2009) and the Kep Archipelago (Bohm, 2019; Tubbs *et al*., 2019, 2020), with IUU fishing considered the most pertinent threat in Kep's coastal waters. Effective management of fisheries and enforcement of fisheries law is essential to the survival of Irrawaddy dolphins across their range. Despite the Kep Archipelago being highlighted as a critical breeding habitat for Irrawaddy dolphins (Tubbs *et al*., 2019), no calf strandings were reported within the archipelago. This may indicate a small population of sexually mature adults and/or low birth rates within the population. Sightings of calves were notably rare, accounting for less than 1% of Irrawaddy dolphin sightings in the archipelago (Tubbs *et al*., 2020).

When assessing sex and age, female juveniles were found to be the most vulnerable to fatal strandings whereas male adults were least vulnerable. This could have significant consequences for the future reproductive success of Irrawaddy dolphins in Kep as population dynamics are shifted by mounting anthropogenic pressures.

Necropsy findings and cause of death

Illegal, unregulated and unreported fishing has been regularly recorded by surveyors within the archipelago during land and boat-based cetacean observation surveys. Together with recorded cases of Irrawaddy dolphin bycatch, these suggest that IUU activity continues to pose a major threat to dolphin populations along the Kep coastline (Bohm, 2019; Tubbs *et al*., 2019).

Some of the individuals we examined showed evidence of harmful intra and/or interspecific interactions including body scars, nicks, notches and a severed caudal fin. These external injuries may have been caused by other Irrawaddy dolphins, sharks or interactions with fishing gear. It is unclear whether they occurred prior to or following death. Injuries prior to death may not have been immediately fatal, although they are likely to have hindered the survival of the afflicted individual, resulting in increased risk of disease, stranding and premature death.

Chemical pollutants such as polychlorinated biphenyls (PCBs) and agricultural fertilisers can build up to toxic levels in the marine environment (Chia, 2000; Todd *et al*., 2010). Bioaccumulation and biomagnification of PCBs, fertilisers and other chemical pollutants in dolphin blubber can severely impact reproductive success and immune responses and increase the likelihood of premature death from disease and infection (Aktar *et al*., 2009; Jepson *et al*., 2016). With riverine inputs from the Giang and the Kampot rivers and a ubiquity of such chemical pollutants in Cambodia, the Kep Archipelago is vulnerable to threats posed by wastewater and agricultural runoff. Although we could not test for such contaminants due to a lack of precision equipment, in-situ veterinary assistance and laboratory support, toxic bioaccumulation may have contributed to dolphin strandings and death and blubber and other soft tissue samples were retained for future analysis. Given the appropriate resources, stable isotope analysis of stomach contents and tissue toxicity levels could also be assessed in future. However, consistent with stable isotope analysis of other Irrawaddy dolphin populations in the Gulf of Thailand and the Andaman Sea (Jackson-Ricketts *et al*., 2018), direct observation of stomach contents confirmed small bony fish, crustaceans and cephalopods as prey species. Noise and plastic pollution were dismissed as possible causes of stranding due to modest vessel traffic within the region and lack of plastic entanglement and ingestion in examined individuals.

Despite current regional threats to the species, the strandings documented here could have been due to natural causes such as illness, infection, internal malfunction, and disease, including age-related diseases. Long-term monitoring of strandings, improvement of a national stranding network (including access to marine mammal veterinarians and adequate sampling equipment and storage) and collaboration among marine mammal research organisations across the Indo-Pacific region is essential to understanding the causes of Irrawaddy dolphin strandings and to ensuring appropriate implementation of conservation legislation and management strategies.

Marine mammal stranding programmes in SE Asia

The report of the third Southeast Asian marine mammal symposium (Hines *et al*., 2015) outlined the activities and findings of marine mammal conservation and research programmes across the Indo-Pacific region. At the time of its publication, China, Japan, Taiwan and Thailand reported well-established national stranding programmes created by fisheries administrations or independent research initiatives. These initiatives attributed their success to awareness, international collaboration, trained personnel, infrastructure, funding and expertise. Most recently, in 2015, the IUCN and Swedish postcode lottery provided funding, training and technical support to Thailand's Department of Marine and Coastal Resources. This support improved data collection and strengthened the capacity of the dolphin stranding network (Smith *et al*., 2016). Programs such as this provide a replicable framework for neighbouring countries such as Cambodia, Myanmar and Vietnam to follow.

Conversely, Brunei, Cambodia, China, Indonesia, Malaysia, Myanmar, the Philippines, and Vietnam reported scarce or unsubstantiated bycatch and strandings data. They also highlighted a need for formal monitoring through a coastal-wide, nationally coordinated stranding response, supported by adequate funding, facilities, researchers and trained personnel. The Department of Fisheries Malaysia identified capacity-building, education and international collaboration as priorities for long-term research and conservation initiatives, extending to the establishment of national strandings networks (Hines *et al*., 2015).

Short-term solutions in the form of online collaboration and communication through forums such as the Global Stranding Network (www.globalstrandingnetwork.com) have been highlighted as useful tools for raising awareness, sharing training materials and protocols and identifying areas of global concern (Gulland & Stockin, 2020). These, combined with funding, expertise and facilities on longer timescales would enable developing nations such as Cambodia to implement an enhanced coastal-wide marine mammal stranding programme, with potential for transnational collaboration. Such a programme could provide valuable information about the histology, virology, parasitology, contaminants, biotoxins, life history and genetics of Irrawaddy dolphins, in addition to informing management strategies for the species and its habitats.

A nationally coordinated response is urgently needed to address threats to coastal Irrawaddy dolphins in Cambodia. This could be led by a statutory body such as the Fisheries Administration or by non-government organisations such as Marine Conservation Cambodia or the World Wildlife Fund for Nature. This effort should focus on responding to and transporting fresh carcasses to qualified veterinarians at fully equipped laboratories as quickly as possible so that the causes of death can be accurately determined. With funding, training and technical support, Cambodia can provide important data on Irrawaddy dolphin strandings, and put effective measures in place to prevent the continued decline of this globally Endangered species.

Conclusions

Between 2017 and 2020, ten fatal Irrawaddy dolphin strandings were recorded within the Kep Archipelago. This study found that stranding events occurred in all seasons throughout the archipelago, with juveniles most vulnerable to fatality. The causes of death could not be confirmed due to lack of trained personnel, facilities and resources, although disease, chemical pollution and bycatch as a result of IUU fishing represent the most likely causes. Establishment of a coastal-wide marine mammal stranding network is urgently needed to record, analyse and mitigate Irrawaddy dolphin strandings. Lessons from stranding programmes in neighbouring countries highlight the importance of adequate funding, facilities, resources and trained personnel in creating and maintaining large-scale stranding networks. We strongly recommend the initiation of a collaborative, coastal-wide strandings network to improve understanding of the anatomy, physiology, pathology and genetics of Irrawaddy dolphins and inform related conservation efforts in Cambodia and across their range.

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Topographical patterns of species composition in a deciduous dipterocarp forest in Kratie Province, Cambodia

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មូលន័យសង្ខេប

យើងបានរុករកពីទម្រង់នៃសមាសភាពប្រភេទព្រៃក្នុងឡូត៍គំរូតាងអចិន្ត្រៃយ៍ទំហំ៩ហិកតា ដើម្បីវាយតម្លៃពីរបាយតាមរយៈកម្ពស់នៃប្រភេទព្រៃល្បោះផ្សេងៗគ្នា ក្នុងខេត្តក្រចេះ ភាគខាងលិចនៃប្រទេសកម្ពុជា។ លំដាប់រយៈកម្ពស់ត្រូវបានកំណត់ពីកំពូលភ្នំដល់ទំនាបលិចទឹកនៃឡូត៍គំរូតាង លក្ខខណ្ឌដី និងព្រៃប្រែប្រួលតាមលំដាប់កម្រិតកម្ពស់។ យើងក៏បានប្រើសន្ទស្សន៍ (index of importance value) សម្រាប់ប្រភេទដែលលុបក្នុងឡូត៍គំរូតាង (0,0៤ ហិកតា) ហើយការវិភាគរង្វាស់បែប non-metric multi-dimensional scaling ត្រូវបានប្រើដើម្បីបង្ហាញពីទម្រង់នៃសមាសភាពប្រភេទ។ ព្រៃល្បោះដែលស្ថិតនៅក្នុងឡូត៍គំរូ ត្រូវបានចែកចេញជា៤ក្រុម (Groups 1–4)។ ប្រភេទសាមញ្ញចំនួន២ បានបង្ហាញពីទម្រង់ចែកដាច់ពីគ្នាតាមបណ្តោយរយៈកម្ពស់គឺ ដើមរាំងភ្នំ (*Shorea siamensis*) ជាប្រភេទមានចំនួនលើសលុបនៅតំបន់ខ្ពស់ (ក្រុម១) និងបន្ទាប់មកគឺ ដើមខ្លុង (*Dipterocarpus tuberculatus*) ដើមផ្ចឹក (*Shorea obtusa*) ឬជួនកាលពពួកដើមឈ្លីក (*Terminalia*) (ក្រុមទី៤) ដែលមានចំនួនលើសលុបនៅតាមវាល និងទំនាបលិចទឹក។ ក្រុមទី៣ត្រូវបានកំណត់ដោយភាពសម្បូរលើសលុបនៃដើមខ្លុង (*D. tuberculatus*) នៅតាមវាល និងទំនាបលិចទឹកដែលពួកវារារាំងដល់ការដុះឡើងវិញនូវប្រភេទផ្សេងៗទៀត។ ក្រុមទី២រួមមានល្បាយនៃ *dipterocarps* ចំនួនបីប្រភេទលាយឡំគ្នាដែលត្រូវបានសម្គាល់ដោយវត្តមាននៃប្រភេទរុក្ខជាតិជាច្រើន ជាមួយនឹងព្រៃស្រទាប់ក្រោមក្រាស់។ ព្រៃប្រភេទនេះគ្រប់ដណ្តប់តាមជើងជម្រាល និងតាមទីវាលខ្ពស់ៗដែលបង្កើតបានជាតំបន់ព្រំដែនរវាងព្រៃក្រុមទី១ និងទី៣–៤។ លទ្ធផលសិក្សារបស់យើងបានបង្ហាញថា ព្រៃល្បោះជាច្រើនប្រភេទអាចដុះលាយឡំគ្នាក្នុងទំហំដីជាច្រើនហិកតា ទោះបីជាវាបានបង្ហាញពីទម្រង់ញែកដាច់ពីគ្នាទៅ

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តាមលំដាប់រយៈកម្ពស់ក៏ដោយ។ ដើម្បីការពារព្រៃល្បោះអោយបានគង់វង្ស គ្រប់សមាសភាពព្រៃតាមលំដាប់រយៈកម្ពស់ (មិនមែនជ្រើសតែប្រភេទដែលមានចំនួនតិចទេ) ត្រូវតែទទួលបាននូវកិច្ចខិតខំប្រឹងប្រែងអភិរក្ស។

Abstract

We explored species composition patterns in a 4 ha permanent sample plot to assess the topographical distributions of various types of deciduous dipterocarp forest in Kratie Province, eastern Cambodia. A toposequence was identified from hill tops to flood plains in the plot and soil and forest floor conditions varied along the toposequence. We also used an index of "importance value" for dominant species in each quadrat (0.04 ha) and non-metric multi-dimensional scaling analysis to visualize patterns of species composition. The deciduous dipterocarp forest in our study plot could be subdivided into four types (Groups 1–4). Two common types clearly separated along the toposequence: strong dominance of *Shorea siamensis* (*raing phnom* in Khmer) on hills (Group 1), and, dominance of *Dipterocarpus tuberculatus* (*khlong*), *Shorea obtusa* (*phchek*), or sometimes *Terminalia* species on plains and flood plains (Group 4). Group 3 was characterized by strong dominance of *D. tuberculatus* scattered throughout the plains and flood plains and suggested limited regeneration of other species. Group 2 comprised a mixture of three dipterocarps characterized by a high number of tree species and large amounts of forest floor vegetation. This forest type occupied foot slopes and the higher sides of the plains, which formed the boundary area between Group 1 and Groups 3–4. Our results indicate that various types of deciduous dipterocarp forests can coexist within a scale of several hectares, although they exhibit separation along the toposequence. To appropriately preserve deciduous dipterocarp forests, all types of forest composition along toposequences (rather than solely types that are limited in abundance) must be included in forest conservation efforts.

Keywords Conservation, dry dipterocarp forest, forest fire, forest floor vegetation, forest type, spatial heterogeneity, topography, tree recruitment.

Introduction

Identification of forest types in combination with their associated topographies and soil conditions is essential for understanding forest ecosystems. In Cambodia, deciduous forests are predominant, comprising 38.2% of the forested area (Ministry of Environment [MoE], 2018). Deciduous forests primarily occur within five provinces (Mondulkiri, Preah Vihear, Kratie, Stung Treng, and Ratanakiri) in northeast Cambodia; these comprise 79.0% of deciduous forests in Cambodia (MoE, 2018). In the Cambodian Forestry Administration (FA) forest classification system, deciduous forests include deciduous (dry) dipterocarp forests and dry mixed deciduous forests (FA, 2018). Deciduous dipterocarp forests are described as "*forêt claire*" (Rollet, 1972) or deciduous dipterocarp forests or woodlands (Rundel, 1999); they exist throughout Indo-Burma (Ashton, 2014) and on skeletal or arid soils up to approximately 600 m elevation in Cambodia (Rollet, 1972; Rundel, 1999).

Deciduous dipterocarp forests have been further subdivided into four types (or subtypes of forest) in Cambodia, each representing distinct combinations of a small number of deciduous species of Dipterocarpaceae (Rollet, 1972). One type of deciduous dipterocarp forest is characterized by dominance of *Dipterocarpus tuberculatus* Roxb. (*khlong* in Khmer), *Shorea obtusa* Wall. ex Blume (*phchek*), and *Terminalia alata* Heyne ex Roth (*chhlik*) of the Combretaceae, which favours plinthite soils ("laterite" in Rollet, 1972). This most predominant type of forest exhibits generally moderate species richness, and a similar floristic structure extends broadly across mainland Southeast Asia (Rundel, 1999). The second forest type is characterized by strong dominance of *Shorea siamensis* Miq. (*raing phnom*), which is the most tolerant of dry habitat conditions among the deciduous species of dipterocarps (Rundel, 1999). This type of forest occupies sites with eroded leptosols (or lithosols) or skeletal soils, such as soils that occur over young basalt flows (Rollet, 1972; Rundel, 1999). The third forest type is characterized by strong dominance of *Dipterocarpus obtusifolius* Teijsm. ex Miq. (*tbeng*) (Rollet, 1972). This type grows on sandy soils that experience seasonal flooding (Rundel, 1999; Hiramatsu *et al*., 2007; Ito *et al*., 2017b). The above three types were also reported by Tani *et al.* (2007). The fourth type exhibits the greatest species richness with characteristic dominance by *Dipterocarpus intricatus* Dyer (*trach*) in upper stature (Rundel, 1999; Hiramatsu *et al*., 2007). Soil conditions under this forest type generally consist of sandy siliceous soil horizons over clay or laterite layers at 20–40 cm depth (Rundel, 1999).

As described above, these four types of deciduous dipterocarp forests have been categorized based on the topography, geology, and soils within the habitat. However, the findings thus far have only described typical habitat patterns; they have not sufficiently examined how these types are distributed in space, at which scale, and what features exist near the boundaries between the different forest types, i.e., transitional forms between the different types of deciduous dipterocarp forests. Determining the spatial distribution patterns of typical and transitional forms, as well as their spatial scales, would provide key information regarding the conservation and sustainable use of these forests. Such data would provide necessary information for conservation planning, such as the extent of area to conserve, the site characteristics to include, and the nature of sustainable forest conditions for each site.

The objective of the present study was to determine the spatial distribution patterns of the first and second types of deciduous dipterocarp forests, and the transitional forms between these within an area of several hectares. The study was conducted on the terrace surface of the Mekong River in Kratie Province, on the east side of the river. Although most topography is flat in Kratie Province, some undulations are present in forested areas. Topographical patterns reflect soil conditions and govern water/groundwater flows, and thus potentially affect tree or understory species composition and stand structure. We established a 4 ha permanent sample plot, assessed spatial heterogeneity in vegetation properties, and examined relationships between species composition (or distribution) and topographic patterns.

Methods

Research site

Our 4 ha study plot (200 × 200 m) included a meteorological observation site and was located 50 km north of the Kratie provincial capital in eastern Cambodia (12.92°N, 106.20°E; elevation: 74–85 m; Fig. 1). The region has a dry season extending from November to April. Annual rainfall (mean ± standard deviation) was 1,643 ± 272 mm during 2000–2010 (National Institute of Statistics, 2012) and mean annual temperature was 27 °C (Iida *et al*., 2016). Tertiary and quaternary sedimentary rocks and basalts underlie forests located on the Mekong River terrace (Ohnuki *et al*., 2008; Toriyama *et al*., 2010; Ohnuki *et al*., 2012). These forests experience a fire regime caused by surface fires almost every year, and the aboveground portion of dead forest floor vegetation almost burns during the dry season. Logging or fuelwood collection was not allowed in the study forest. However, illegal logging did occur occasionally. There was no grazing.

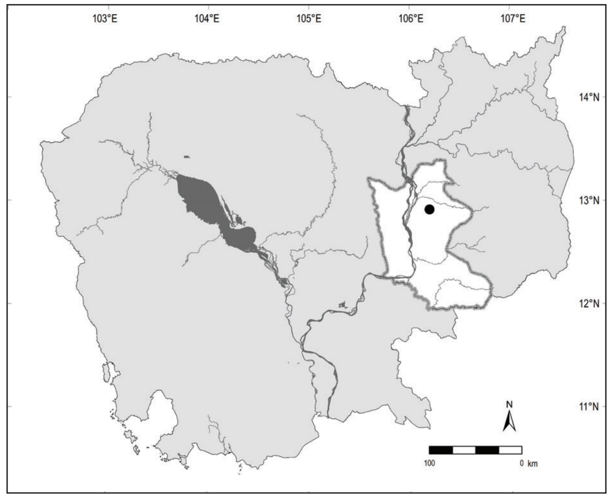

Fig. 1 Location of study site (solid circle) in Kratie Province (white area), Cambodia. Dark gray areas and lines indicate water bodies and rivers, respectively.

The study plot encompassed a toposequence from hill tops (i.e., elevated sections in the southeastern portion of the plot) to foot slopes, plains and flood plains (i.e., flat areas in the northwestern portion of the plot). The main stream flows from west to northeast, and two small streams enter from the south (Fig. 2A). The soil types were outlined by Ito *et al*. (2017a) (Fig. 2B). Soil thickness measurements were conducted using a dynamic cone penetrometer at 41 points in and around the study plot (Ohnuki *et al*., 2008; adding 17 points to Ito *et al*., 2017a; Fig. 2C). Topography, soil type, and soil thickness were associated with each other in the study plot (Fig. 2D). The hills contained leptosols (Food & Agriculture Organization soil classification), in which the basaltic bedrock was often exposed. Leptosols are shallow (<1 m deep and primarily <50 cm deep) debris soils (Figs. 2B–C; Ohnuki *et al*., 2012). Plinthosols (i.e., clay soils that possess a hard plinthite layer with large accumulations of iron) are distributed in the foot slopes and plains, except near small streams (Ohnuki *et al*., 2012). In the area of plinthosols located at the foot slope near the arenosol boundary, fine debris and large weathered basalt debris (probably transported from the hill tops) occur at a thickness of >50 cm within a 1 m deep soil pit (Ohnuki *et al*., 2014). Arenosols (i.e., thick sandy soils) are located in the flood plains and plains near the streams. Coarse-rounded quartzite gravel has been found on the ground surface along the stream (Ohnuki *et al*., 2022). Plinthosols and arenosols exhibit significantly deeper soils (1.0–2.5 m deep), compared

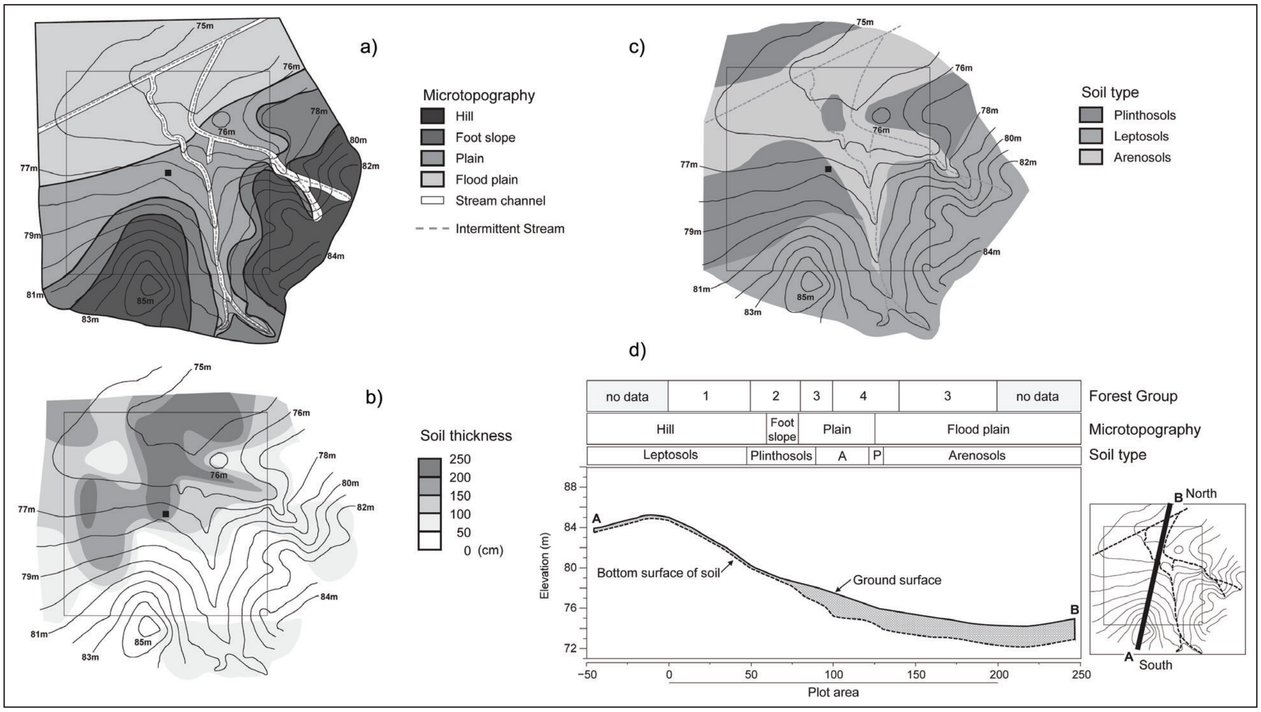

Fig. 2 Topographical and soil conditions of study plot. A) Microtopographic classification, B) soil types, C) soil thickness, and D) topographic cross section. Soil type and soil thickness are modified from Ito *et al*. (2017a). Dashed gray lines indicate intermittent streams. Square boundary line and solid black symbol indicate 4 ha study plot (200 × 200 m) and meteorological flux observation tower, respectively.

with leptosols (Figs. 2B–C; Ito *et al*., 2017a). Water storage capacity in the study plot is directly proportional to soil thickness, considering an effective porosity identical to the three soil types (0.15 m^3 m^{-3}, Ohnuki *et al*., 2008).

Tree census

We divided the 4 ha plot into 1,600 quadrats each measuring 5 × 5 m. Within the plot, we recorded the girth of all standing woody stems with values ≥5 cm at 1.3 m above ground level (diameter at breast height, DBH) to the nearest 1 mm. These data were collected in the dry season of mid-February 2017. We also identified trees to species level and recorded the position of each individual based on the 5 × 5 m quadrat location. Coppiced stems were included in basal area and stem density measurements. Scientific names of species are presented in Annex 1. Though the glabrous type and hairy type of *T. alata* have not been confirmed as distinct species, they differ substantially in habitat and leaf phenology (Ito *et al*., 2017a) and are treated separately for convenience in this paper. Stand structure parameters calculated from tree census data included basal area (m^2 25 m^{-2}), stem density (number of stems 25 m^{-2}) and maximum stem diameter (cm) for all species in each 5 × 5 m quadrat.

Forest floor vegetation census

As an index of aboveground forest floor vegetation biomass, we investigated spatial variation in the height of understory vegetation (hereafter, understory height) at 747 points within the 4 ha plot on 4–5 September 2011. Understory height (cm) was measured by reading the height of any plant (primarily grasses) touching a vertically standing measuring rod. Data were interpolated onto a 0.5 m mesh grid and then averaged for each 5 × 5 m quadrat.

Aboveground forest floor biomass was destructively investigated on 20 November 2012. Floor vegetation was sampled in 0.5 × 0.5 m areas at the corners of sixteen 50 × 50 m quadrats within the 4 ha plot except in the centre of the plot (location of our meteorological tower). Each sampling area was located 2 m forward from the corner of quadrats towards the flux tower. This was to avoid the influence of foot traffic and concrete-post setting on sampling data. Following sorting of samples into the leaves of shrubs or juvenile trees, the stems and branches of shrubs or juvenile trees, and grasses, these were oven-dried and weighted.

Fire regime census

The spatial distribution of the fire regime was examined from 29 January to 1 February 2014. We recorded whether the base of each standing tree had been burnt or not and then calculated the percentage of burnt trees in each of four hundred 10 × 10 m quadrats constituting the 4 ha plot. In quadrats without standing trees, we visually determined the percentage of burnt areas. The fire regime was also directly observed from 10 February to 10 March in 2012 and 2013 at the corners of sixteen 50 × 50 m quadrats within the 4 ha plot except for the centre of the plot. In these instances, we recorded whether the area within 5 m in four directions from the fixed observation point was burning or not.

Species composition analysis in 20 × 20 m subplots

For species composition analyses, we pooled tree census data from 16 neighbouring 5 × 5 m quadrats and treated them as a single 20 × 20 m subplot (i.e., 100 total subplots within the 4 ha plot). The dominant tree species was defined as the species with the highest importance value (IV index) for each 20 × 20 m subplot. IV indexes for every species in each quadrat were calculated as follows:

$$IV_i = (\%N_i + \%G_i) / 2$$

where $\%N_i$ is the proportion of stems of species *i* relative to the total number of stems for all species, and G_i is the proportion of basal area of species *i* relative to the total basal area of all species (Nguyen & Baker, 2016). To compare our data with the results of previous studies, we calculated IV indexes only when stems with DBH ≥10 cm were selected.

To explore patterns of species composition for each 20 × 20 m subplot, we employed non-metric multidimensional scaling (NMDS) (Kenkel & Orlóci, 1986) with the "vegan" package (Oksanen *et al*., 2019) in R (R Core Team, 2020). Bray–Curtis dissimilarity (Beals, 1984) in species composition was calculated based on the IV indexes, which was used to identify grouping patterns of quadrats using NMDS. We used the "vegdist" and "metaMDS" functions for these analyses.

To determine groups of quadrats, we used hierarchical cluster analysis with the "cluster" package (Maechler *et al*., 2019) in R (R Core Team, 2020). Bray–Curtis dissimilarity was also used for the hierarchical cluster analysis, wherein the quadrats were grouped based on the number of groups objectively determined with the largest silhouette value. We used the "hclust" and "silhouette" functions for these analyses.

One-way analysis of variance and post hoc Tukey-Kramer honest significant difference tests were used to evaluate differences in understory height among the 20 × 20 m subplots with different dominant tree species. These were also used to determine differences in basal area, stem density, the number of total species, the number of dipterocarp species (or number of non-dipterocarp species) in each subplot, as well as understory height and aboveground understory biomass among the NMDS-identified groups mentioned above. The size (DBH) distributions of the three dipterocarp species and other non-dipterocarp species were examined using NMDS-identified groups. This analysis was conducted in JMP statistical software (ver. 10.0, SAS Institute Inc., North Carolina, USA).

Results

Forest properties and spatial characteristics

For free-standing stems with DBH ≥5 cm, our study plot comprised 13.76 m^2 ha^{-1} in basal area, 555.5 stem ha^{-1} for stem density, and a total of 46 tree species. For free-standing stems with DBH ≥10 cm, the study plot comprised 12.88 m^2 ha^{-1} in basal area, 358.8 stem ha^{-1} in stem density, and 36 tree species in total (Table 1, Annex 1).

The spatial distribution of three forest properties (basal area, stem density and maximum stem diameter) are shown in Figs. 3A–3C. Of the 1,600 quadrats (5 × 5 m), 999 (62.4% of the total) contained at least one tree individual with DBH ≥5 cm (hereafter referred to as with-tree quadrat). Quadrats not including individuals with DBH ≥5 cm (n = 601) were frequently found in the northwest area of the plot; fewer such quadrats were found in the southeast area (Fig. 3). Based on the same three forest properties (basal area, stem density, and maximum stem diameter), the plot was also generally divided into two areas (i.e., northwest and southeast). For with-tree quadrats, basal area was slightly higher in the northwest area (Fig. 3A), stem density was slightly higher in the southeast area (Fig. 3B) and maximum stem diameter was considerably higher in the northwest area (Fig. 3C). In terms of microtopography (Fig. 2A), stem density was lower in the flood plains and higher on hills (Fig. 3B), while maximum stem diameter was greater on flood plains and smaller on hills (Fig. 3C).

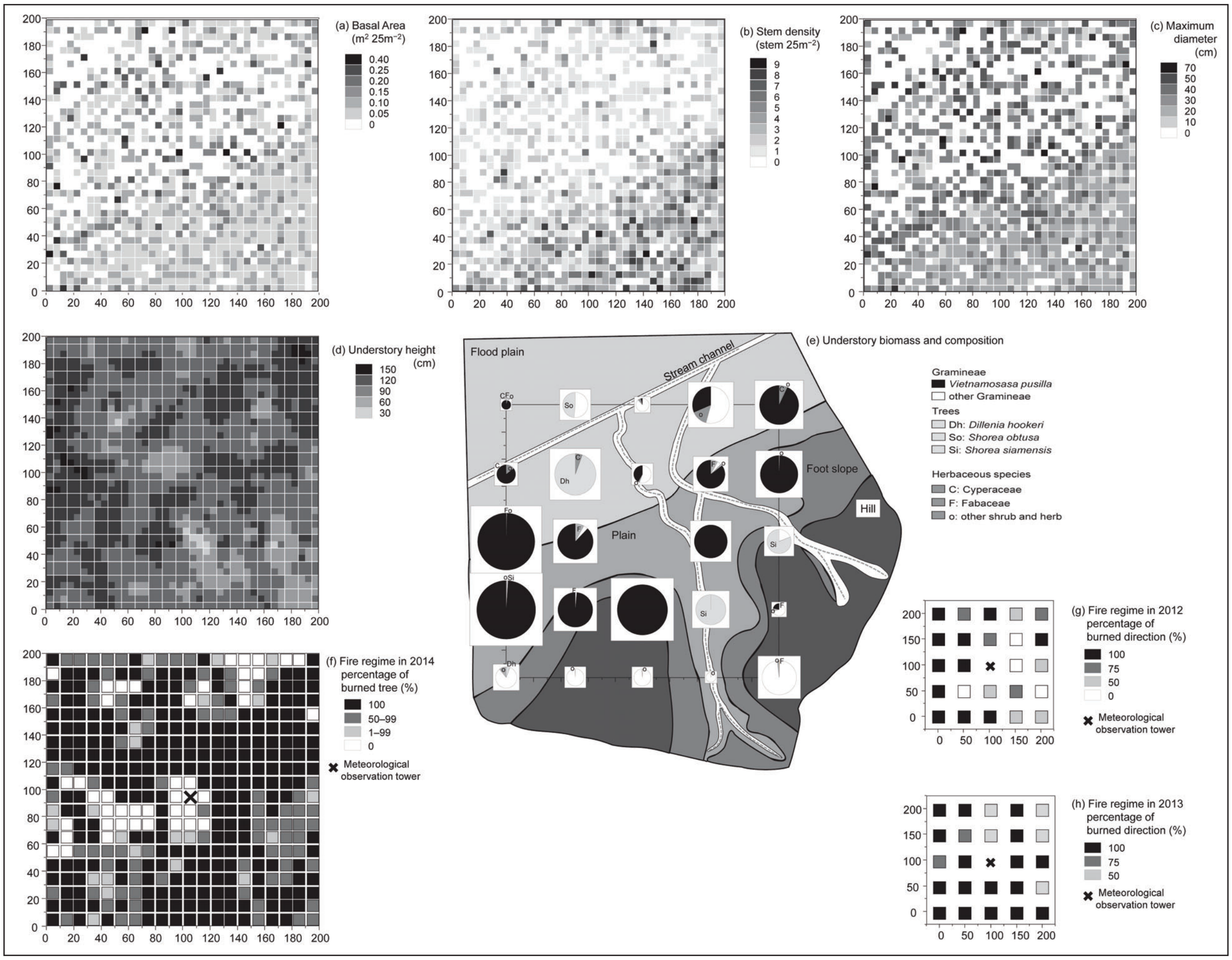

Fig. 3 Spatial distribution of selected forest properties in the study plot. A) Basal area, B) stem density, C) maximum DBH, D) understory height, E) understory biomass and its composition, F) fire regime in 2014, G) fire regime in 2012, and H) fire regime in 2013. The scales of pie charts in Fig. 3E are proportional to the total amount of understory biomass (Annex 2). In Fig. 3F, the area around the observation tower has been cleared to prevent the spread of fire.

Table 1 Structural properties of deciduous dipterocarp forest trees at study site in Kratie Province, Cambodia.

Metric / species	5–10 cm DBH	≥10 cm DBH	Total
Basal area (m² ha⁻¹)	0.88	12.88	13.76
Dipterocarpus tuberculatus	0.07	4.17	4.24
Shorea obtusa	0.01	2.40	2.41
Shorea siamensis	0.52	2.19	2.72
Stem density (stems ha⁻¹)	197.3	358.8	556.0
Dipterocarpus tuberculatus	14.8	91.5	106.3
Shorea obtusa	3.5	43.8	47.3
Shorea siamensis	114.3	109.3	223.5
No. of species (spp. 4 ha⁻¹)	38	36	46

Topographical locations were clearly linked to forest floor vegetation (Figs. 3D–E). Lower understory heights were primarily found in the hills and flood plains (Fig. 3D). The spatial distribution of understory height varied from 15 to ca. 140 cm tall (Fig. 3D). Our field observation and destructive survey of the biomass of understory vegetation indicated that in the plain and foot slope, the top layer of herbaceous communities primarily consisted of dense dwarf bamboo grass (*Vietnamosasa pusilla*), whereas the lower layer often consisted of other herbaceous species belonging to the Gramineae and Fabaceae (Fig. 3E). The understory biomass in these areas ranged from 3.5 to 7.2 Mg ha⁻¹. In the flood plain, *V. pusilla* and other Gramineae were abundant, but their biomass was not significant (1.1–5.0 Mg ha⁻¹). A small colony of

Dillenia hookeri (*phlou bat*; approximately 50 cm tall) and herbaceous species in the Cyperaceae were also observed near the main stream. Saplings of *S. obtusa* were found in one location (X50, Y200). In the southeast area, the grass layer was generally composed of herbaceous species of Gramineae (1.2–4.2 Mg ha^{-1}). *Shorea siamensis* saplings were found in some parts of this area. *Cycas siamensis* (*brong*) was present, but rare and not found in the destructive sampling plots. Details of understory vegetation biomass obtained from the destructive survey in 24 sites are shown in Annex 2. The spatial distribution of fire is shown in Figs. 3F–H. The percentage and distribution of areas burnt varied from year to year. Visual comparisons of these spatial distributions indicated that understory height and biomass appeared to be less associated with the frequency of fire.

Spatial distributions of dominant dipterocarp species and other species

The study plot contained three dominant dipterocarp species. These were *D. tuberculatus*, *S. obtusa*, and *S. siamensis*, which respectively comprised 30.8%, 17.5% and 19.7% of the total basal area of the plot and 19.1%, 8.5% and 40.2% of the total number of stems, respectively (Table 1, Annex 1). *Dipterocarpus tuberculatus* was evenly distributed in the plot, although its basal area was larger in the northwest area (Fig. 4A). *S. obtusa* was scattered in the northwest area (Fig. 4B) and *S. siamensis* was distributed throughout the southeast area (Fig. 4C).

The maximum number of tree species that appeared in a 5 × 5 m quadrat was five (Fig. 5A). Among the with-tree quadrats (n = 999), the mean number of tree species present in a quadrat was 1.6 and 570 quadrats (57.1%)

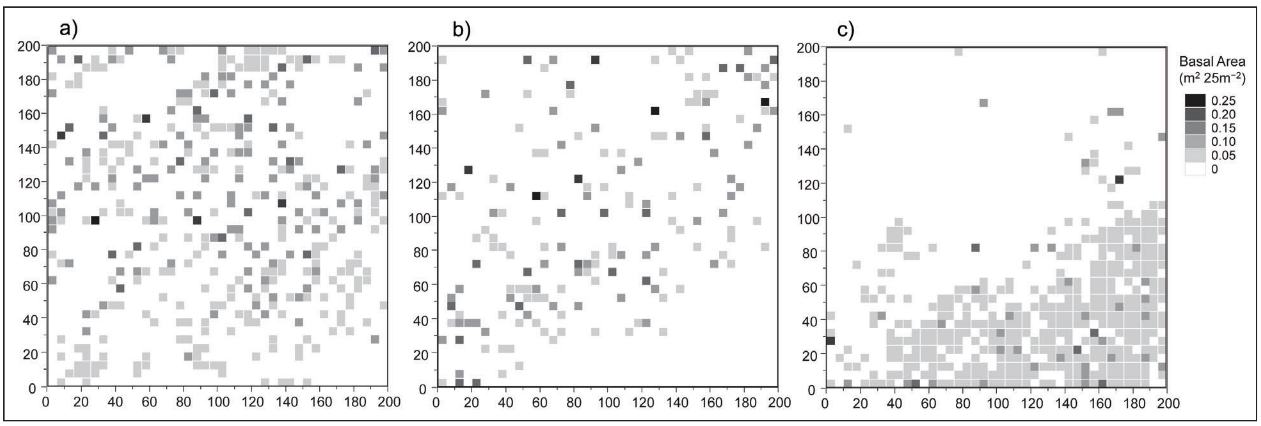

Fig. 4 Spatial distributions of predominant dipterocarp species in study plot. Basal areas of A) *Dipterocarpus tuberculatus*, B) *Shorea obtusa*, and C) *Shorea siamensis*.

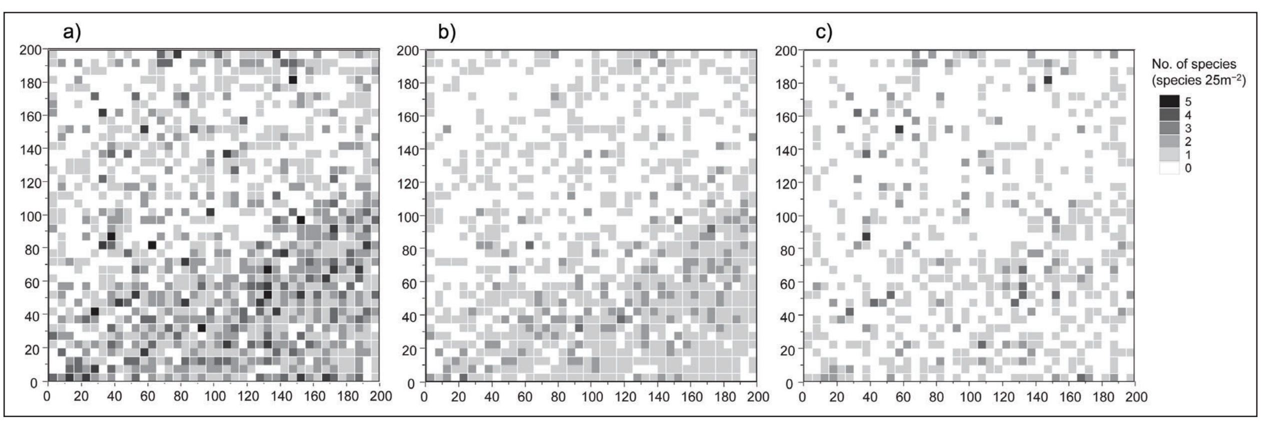

Fig. 5 Spatial distributions of species richness in study plot. A) All species, B) three dominant dipterocarp species, and C) all other species.

contained only one species (Fig. 5A). The numbers of quadrats containing *D. tuberculatus*, *S. obtusa* and *S. siamensis* were 369, 169 and 428, respectively (Figs. 4A–4C). The three dominant dipterocarp species were rarely distributed together, in co-occurring in only six quadrats (Fig. 5B). Among the with-tree quadrats, at least one of the three dominant dipterocarp species occurred in 825 quadrats (82.6%) (Fig. 5B). Of the 129 quadrats (12.9%) in which two species of dipterocarps occurred, 76 quadrats (58.9% of the 129 quadrats) included *D. tuberculatus* and *S. siamensis*, 28 quadrats (21.7%) included *S. obtusa* and *S. siamensis* and 25 quadrats (19.4%) included *D. tuberculatus* and *S. obtusa*.

Other non-dipterocarp species (43 species in total) occurred in 521 (52.1% of total) quadrats among the 999 with-tree quadrats. On rare occasions, 3–4 non-dipterocarp species appeared in a quadrat (Fig. 5C).

Dominant species and species composition groups (IV index and NMDS analysis)

Six tree species were considered dominant based on the IV index for each 20 × 20 m subplot (Fig. 6). The dominant tree species in the largest number of plots was *D. tuberculatus* (n = 46), which dominated a large portion of the northwest area. The second most dominant tree species in the subplots was *S. siamensis* (n = 30), which dominated all of the southeast area. The third most dominant tree species in the plots was *S. obtusa* (n = 16), and the plots dominated by this species occurred near the boundary between southeastern and northwestern areas. These three dipterocarp species were dominant in 92% of the subplots. The other eight subplots were dominated by three *Terminalia* spp. The glabrous type of *T. alata* (n = 3) was dominant near the boundary between the two main areas, similar to *S. obtusa*. The hairy types of *T. alata* (n = 3) and *T. mucronata* (n = 2) were occasionally dominant near the northwest corner of the study plot. Understory height was significantly lower in subplots dominated by *S. siamensis*, compared with subplots dominated by other species (F = 54.4, p<0.0001).

Hierarchical cluster analysis determined four distinct groups among the 20 × 20 m subplots. NMDS analysis showed that Group 1 was tightly clustered (Fig. 7A), dominated by *S. siamensis* without exception (Fig. 7B, Table 2) and occupied the southeast area (Fig. 7C). Group

Table 2 Characteristics of groups separated in the non-metric multi-dimensional scaling analysis.

	Group			
	1	2	3	4
Dominant species*	*S. siamensis* (24)	*D. tuberculatus* (10), *S. obtusa* (10), *S. siamensis* (6), *T. alata* (glabrous) (3)	*D. tuberculatus* (18)	*D. tuberculatus* (13), *S. obtusa* (6), *T. alata* (hairy) (3), *T. mucronata* (2)
No. of subplots	24	34	18	24
Microtopography	Hills	Foot slope / upper plain	Flood plain / lower plain	Flood plain / lower plain
Stem density† (stems 0.04 ha^{-1})	43.3 ± 8.5 ^{a} [27–65]	20.3 ± 10.4 ^{b} [8–51]	11.3 ± 5.1 ^{c} [5–25]	12.1 ± 4.8 ^{c} [6–25]
Basal area† (m^{2} 0.04 ha^{-1})	0.55 ± 0.09 ^{ab} [0.39–0.72]	0.62 ± 0.21 ^{a} [0.22–1.06]	0.47 ± 0.17 ^{b} [0.16–0.76]	0.51 ± 0.19 ^{ab} [0.11–0.88]
No. of species† (0.04 ha^{-1})	5.9 ± 1.8 ^{ab} [3–10]	6.6 ± 2.6 ^{a} [3–15]	4.6 ± 1.5 ^{b} [1–7]	6.0 ± 1.5 ^{ab} [4–9]
No. of dipterocarp species† (0.04 ha^{-1})	2.3 ± 0.7 ^{b} [1–3]	2.7 ± 0.5 ^{a} [2–3]	1.7 ± 0.5 ^{c} [1–2]	2.0 ± 0.5 ^{bc} [1–3]
No. of non-dipterocarp species† (0.04 ha^{-1})	3.6 ± 1.4 ^{a} [1–7]	3.9 ± 2.4 ^{a} [1–12]	2.9 ± 1.4 ^{a} [0–5]	3.9 ± 1.5 ^{a} [2–6]
Understory height† (cm)	69 ± 16 ^{c} [29–127]	87 ± 16 ^{a} [16–135]	82 ± 16 ^{b} [25–123]	84 ± 19 ^{b} [36–142]
Aboveground understory biomass (Mg ha^{-1})	3.0 ± 1.4 ^{a} [1.2–6.2]	4.4 ± 1.3 ^{a} [2.6–7.2]	2.6 ± 1.7 ^{a} [1.1–7.0]	4.3 ± 1.3 ^{a} [1.6–7.0]

* Figures in parentheses indicate the number of subplots dominated by that species. † Values represent mean ± standard deviation [range]. Figures on the same row with different superscript letters indicate significant differences (p<0.05).

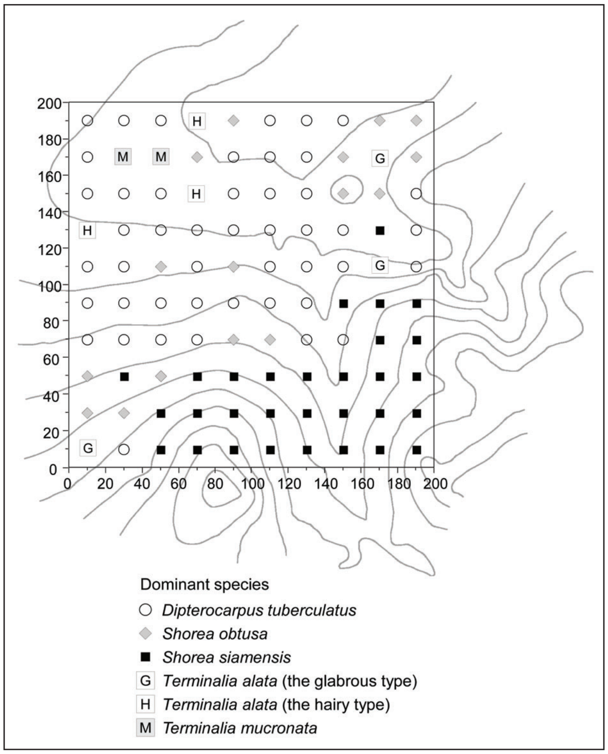

Fig. 6 Spatial distributions of the dominant tree species for each 20 × 20 m subplot. Gray lines indicate elevation contours.

3 was also clustered (Fig. 7A), dominated by *D. tuberculatus* without exception (Fig. 7B, Table 2) and scattered in the northwest area (Fig. 7C). Groups 2 and 4 were more diffusely arranged (Fig. 7A) and dominated by various species (Fig. 7B, Table 2). Group 2, in which *S. siamensis* and the glabrous type of *T. alata* occasionally dominated, in addition to *D. tuberculatus* and *S. obtusa*, was distributed in the border between the northwest and southeast areas. In contrast, Group 4, where the hairy type of *T. alata* and *T. mucronata* occasionally dominated in addition to *D. tuberculatus* and *S. obtusa*, was scattered in the northwest area (Fig. 7C, Table 2).

Stem density was higher in Group 1 in the southeast area, followed by Group 2 at the border between northwest and southeast areas. Values of stem density were

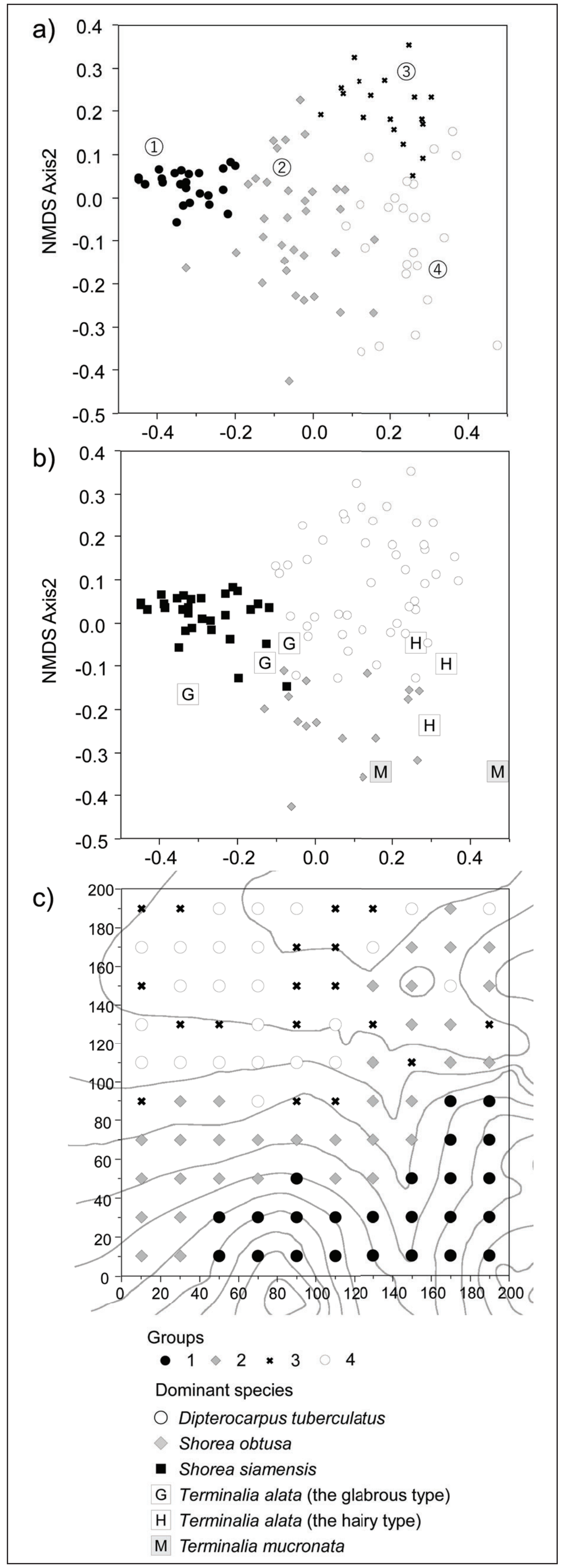

Fig. 7 (right) Non-metric multidimensional scaling (NMDS) based on the species compositions of 100 subplots. A) NMDS by identified groups (stress value = 0.137), B) NMDS by dominant species, and C) spatial distributions of groups with elevation contours (gray lines).

lower in Groups 3 and 4 in the northwest area. Basal area did not differ in a manner similar to stem density among groups; it was smaller in Group 3, which was only dominated by *D. tuberculatus*, and significantly differed from Group 2 (Table 2). The number of species was larger in Group 2 and smaller in Group 3. The number of non-dipterocarp species did not differ among groups; thus, differences in the total number of species between groups were attributed to differences in the number of dipterocarp species (Table 2). Understory height was significantly larger in Group 2, followed by Groups 3 and 4; it was lowest in Group 1 (Table 2).

The size (DBH) distributions of the dipterocarp and non-dipterocarp species (*T. alata* and others) are shown according to group (Fig. 8). Although *D. tuberculatus* was found in all four groups, the shape of the DBH distribution differed between Group 1 and the other groups. Group 1 had no large-diameter trees, whereas it contained many small-diameter trees (Fig. 8A). In the other groups, the peak of the diameter distribution was in the range of 15–30 cm (Fig. 8A). For the size distribution of *S. obtusa*, a peak distribution in the medium size class was observed for all groups (Fig. 8B). The size distribution of *S. siamensis* differed markedly among groups (Fig. 8C). Very few *S. siamensis* individuals were present in Groups 3 and 4, whereas many such individuals were found in Group 1. In Groups 1 and 2, when sufficient individuals were present, the size distribution exhibited an "L" shape; smaller size was associated with greater number of individuals. Populations of the glabrous type of *T. alata* were commonly found in Groups 1 and 2, but the size distribution was not L-shaped (Fig. 8D). The hairy type of *T. alata* was found rather evenly in each class of Group 4, although there were not enough individuals to determine the size distribution (Fig. 8D). The overall size distribution of the other non-dipterocarp species was L-shaped, except for Group 3 (Fig. 8E). However, the number of individuals of each species was small, and only *Xylia xylocarpa* in Group 2 could be regarded as having an L-shaped distribution on a species basis. The maximum DBH for each non-dipterocarp species is listed in Annex 1.

Discussion

Deciduous dipterocarp forest at the study site

The overwhelming dominance of one or two deciduous dipterocarp species at the stand level is considered a defining feature of deciduous dipterocarp forests (Bunyavejchewin, 1983; Bunyavejchewin *et al*., 2011; Nguyen & Baker, 2016). Our study site was also characterized by the local existence of one or two of the three deciduous dipterocarp species (Fig. 5B). We expected our study plot would contain two types of deciduous dipterocarp forests: one forest dominated by *D. tuberculatus* and *S. obtusa* (=the first type in the introduction), and another forest dominated by *S. siamensis* (=the second type in the introduction). The former type corresponded to Group 4 in our NMDS analysis and occurred on the plains and flood plains, whereas the latter corresponded to Group 1 and exclusively occurred on hills (Table 2, Fig. 7). In addition to these two common types, our NMDS analysis suggested the existence of Group 3, which was strongly dominated by *D. tuberculatus*, and Group 2, which was a mixture of all three dipterocarp species (Table 2). Our study also clarified the distributions of Group 3 and Group 2: Group 3 was distributed in a patchy manner within Group 4, and Group 2 occupied the foot slopes between Group 4 and Group 1 (Fig. 7).

Group 4 has been reported in several studies of deciduous dipterocarp forest in Cambodia, including in the Phnom Prich Wildlife Sanctuary (Pin *et al*., 2013), in the Mondulkiri Protected Forest (Pin *et al*., 2013), and in Kratie Province (DDF3 in Tani *et al*., 2007). A forest type similar to Group 1, dominated by *S. siamensis*, has been reported in Mondulkiri Province (DDF2 in Tani *et al*., 2007). However, this forest type was not exactly the same as ours because several indicator or dominant species (*Quercus kerii*, *Dipterocarpus obtusifolius* and *T. mucronata*) were absent from Group 1 in our study. There is also a deciduous dipterocarp forest study in south-western Cambodia (Phnom Samkos Wildlife Sanctuary), but the species were not described and the details of the forest type are unknown (Wood, 2012). To the best of our knowledge, the existence of Group 2 and Group 3 in Cambodia is unique to our study.

Comparison of species composition with deciduous dipterocarp forests in continental Southeast Asia

The species composition of our study site is similar to other deciduous dipterocarp forests in continental Southeast Asia in terms of dominant dipterocarp species, but differs in several respects. The species composition (Annex 1) and forest characteristics (Tables 1–2) of our site were most similar to deciduous dipterocarp forests in Yok Don National Park in central Vietnam (Nguyen & Baker, 2016), which is located 170 km due east of our study site. Compared to the Doi Inthanon National Park, Chiangmai, Thailand, our site differed from the pine-dipterocarp forest in the intermediate zone (850–1400 m above sea level [asl]) in terms of the absence of *Pinus* spp., and from the deciduous dipterocarp forest in the lowlands (400–850 m asl) in terms of high abun-

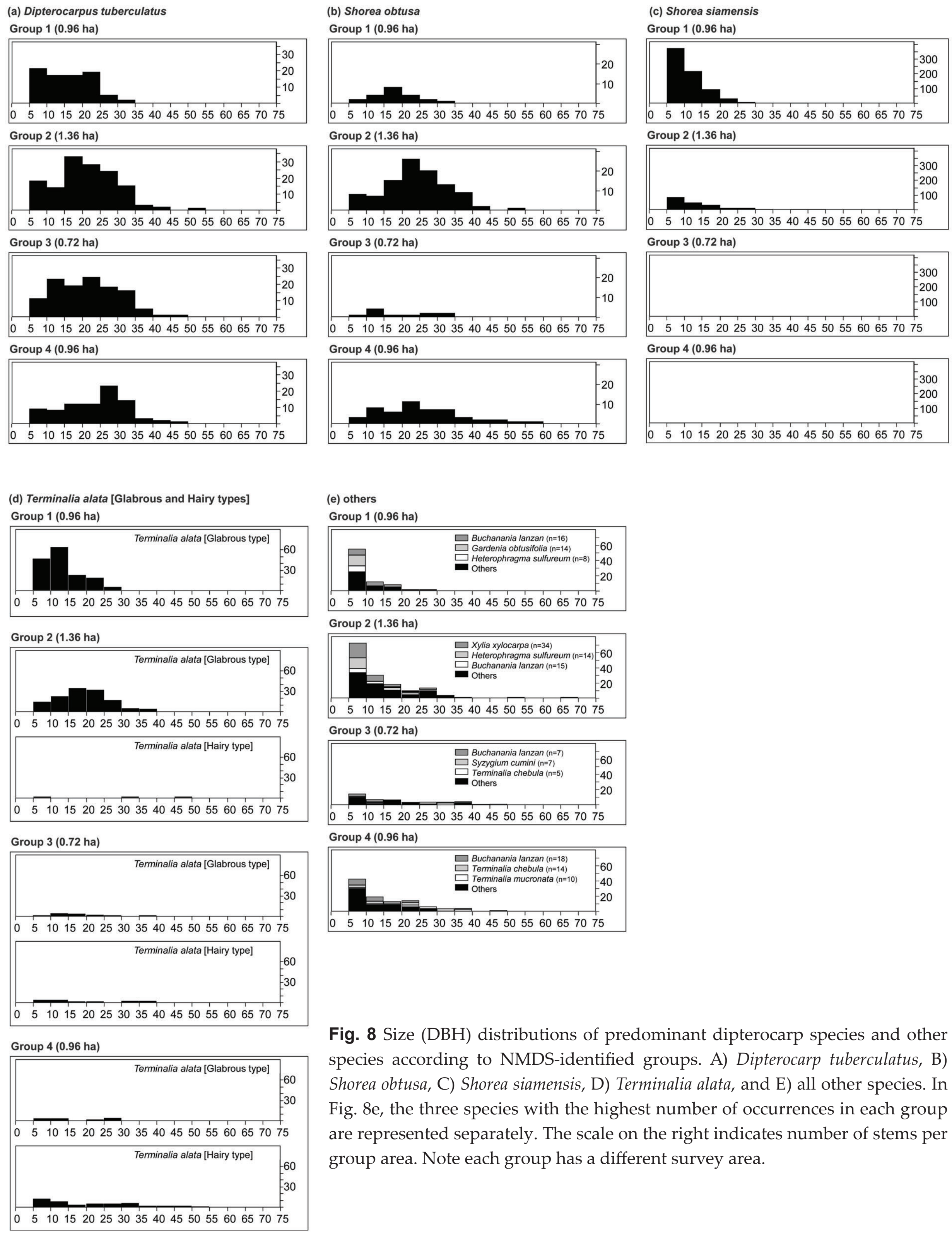

Fig. 8 Size (DBH) distributions of predominant dipterocarp species and other species according to NMDS-identified groups. A) *Dipterocarpus tuberculatus*, B) *Shorea obtusa*, C) *Shorea siamensis*, D) *Terminalia alata*, and E) all other species. In Fig. 8e, the three species with the highest number of occurrences in each group are represented separately. The scale on the right indicates number of stems per group area. Note each group has a different survey area.

dances of *D. tuberculatus* and accompanying species (i.e., low abundance of *Canarium subulatum*) (Robbins & Smitinand, 1966; Bunyavejchewin, 1983; Teejuntuk *et al*., 2002; Nguyen & Baker, 2016). The overall difference of our study site from deciduous dipterocarp forests in northern Thailand involves the non-universal presence of *S. obtusa*, i.e., S. obtusa was not present everywhere in our study site (Santisuk, 1988).

Although the topographical properties of our study site were similar to those in the Sakaerat deciduous dipterocarp forest of northeastern Thailand (i.e., frequent comparatively low, undulating hills with a slightly dry climate and shallow soils), the species composition differed from the Sakaerat forest in terms of the absence of *Shorea roxburghii*, presence of *D. tuberculatus* (Sahunalu, 2009) and absence of *D. intricatus* (Sakurai *et al.*, 1998). Our study forest also differs from a semi-Indaing forest (*D. tuberculatus* forest in Burma, a tropical dry deciduous forest based on the Burmese classification), in terms of the absence of teak *Tectona grandis* (Stamp, 1924; Hundley, 1961; Davis, 1964).

Our observation of co-occurring dominant deciduous dipterocarp species is also consistent with the species compositions of other forests in the region. For example, in lowland Thailand (Bunyavejchewin, 1983; Rundel & Boonpragob, 1995; Teejuntuk *et al*., 2002) and Vietnam (Nguyen, 2009 and references therein), several associations of dominant dipterocarp species (i.e., dominance type: Bunyavejchewin, 1983) have been reported: *S. obtusa* and *S. siamensis*; *D. tuberculatus* and *S. obtusa*; and combinations of the three species. However, the combination most frequently observed in the present study was the combination of *D. tuberculatus* and *S. siamensis*, likely because the wide distribution range of *D. tuberculatus* in the study plot included hill tops to which *S. siamensis* was limited (Figs. 4A, 4C).

Elevational differences in the distribution of these dominance types have been found in Thailand (Bunyavejchewin, 1983). For instance, the *S. siamensis* type, which is similar to our Group 1, was distributed at lower elevations around 280 m, while the *D. tuberculatus-S. obtusa* type, which is similar to our Group 4, was reported as occurring at altitudes of 300 to 900 m (Bunyavejchewin, 1983). However, our study site lacked elevational differences among the three dipterocarp species; more specifically, *S. siamensis*, *D. tuberculatus* and *S. obtusa* were separated within a toposequence with an elevational difference of 10 m.

Group 2 noticeably differed from our other groups in that the three species of dipterocarps were often equally dominant (Table 2). It is also similar to the forest type reported by Ogawa *et al*. (1961) as mixed savanna forest, which was later renamed mixed dry dipterocarp association (Bunyavejchewin, 1983). This forest type is characterized by component species which are numerous and well-mixed, with no distinct dominants (Ogawa *et al*., 1961). The most commonly associated genera within mixed savanna forests are *Canarium*, *Gardenia*, *Heterophragma*, *Lannea*, *Terminalia*, *Vitex* and *Xylia* (Ogawa *et al*., 1961), although our site also included *Adina*, *Lagerstroemia*, *Mangifera*, *Parinarium*, *Saurauia* and *Sindora* (Annex 1). Group 2 occupied the foot slopes on the border between the plains and hills. Its soil conditions were consistent with previous descriptions: commonly sandy clay loam or frequently underlaid by fine sandy loam on plains, associated with stony sandy soils on hillsides (Ogawa *et al*., 1961; Bunyavejchewin, 1983). Other striking features of Group 2 included larger basal area values, higher understory height and higher species richness (Table 2). The large basal area and high understory height suggest rich biomass in Group 2, which is consistent with a previous finding that the growth of rubber trees was highest on foot slopes along a toposequence (Okubo & Takeuchi, 1998).

Transitions between groups

One of our study objectives was to identify the forms of transition between deciduous dipterocarp forest types. Sharp boundaries often occur between different types of dominant dipterocarp species (Nguyen & Baker, 2016 and references therein), which is consistent with the separation of Group 1 from our other three groups (Fig. 7C). A key finding was that Group 2 functioned as the boundary area between Groups 1 and 4 (Fig. 7C). This separation of forest types was attributable to toposequence at a scale of several hundred meters (Fig. 2D), as reported in Kampong Thom Province (Hiramatsu *et al*., 2007) and peninsular Thailand (Ohkubo & Takeuchi, 1998). Group 3 was scattered along with Group 4 in the plains and flood plains (Fig. 7C). The reasons for this scattered distribution are discussed below, along with factors responsible for the low abundances of tree species other than *D. tuberculatus* in Group 3.

Specific distribution patterns of deciduous dipterocarp and driving factors

Absence of S. siamensis in plains vs. light environment and fire intensity

Shorea siamensis was noticeably absent from the lower plain and flood plain (Figs. 4C, 8C). Marod *et al*. (2004) reported that the survival and growth rates of *S. siamensis* seedlings were dramatically greater in gaps than under the closed canopy. Understory height is expected to have a monotonically increasing relationship with biomass of forest floor vegetation, implying a negative correlation between understory height and light transmittance. The light environment near the ground surface in the plain and flood plain may involve excessive shade for survival of *S. siamensis* seedlings, although this needs to be confirmed by seedling trials. Variation in understory biomass, i.e., fuel, also leads to differences in the intensity of combustion. The understory height in our study area (15–140 cm, Fig. 3D) corresponded to a high to very high fuel hazard (McCarthy *et al*., 1999), whereas the understory biomass (1.1–7.2 Mg ha^{-1}, Fig. 3E, Annex 2) corresponded to low to moderate surface fine fuel hazard (McCarthy *et al*., 1999). Fire regimes in deciduous dipterocarp forests have been reported in detail for north and northeast Thailand (Stott, 1986). Fire intensity may appear to act as a critical environmental filter of tree species composition in our study plot, as reported previously for deciduous dipterocarp forests (Rundel & Boonpragob, 1995; Nguyen *et al*., 2019). For instance, Nguyen *et al*. (2019) demonstrated that juveniles of *S. siamensis*, *S. obtusa* and *D. obtusifolius* require a comparatively long fire-free period to reach their fire-escape size, whereas juveniles of *D. tuberculatus* can become saplings despite an annual fire regime. The thin outer bark of low-height (<3 m) trees was noted as a possible reason for the fire vulnerability of *S. siamensis* (Nguyen *et al*., 2019). In the present study, understory height differed significantly between hill tops, where *S. siamensis* is intensively distributed, and other areas (Table 2). The absence of *S. siamensis* was most likely because of light conditions, fire intensity, or both, depending on the amount of forest floor vegetation.

Low prevalence of trees (or of trees other than D. tuberculatus) in plains vs. spatial heterogeneity in fire intensity

Our Group 3, which occurred on the plains and flood plains, included fewer tree populations of species other than *D. tuberculatus* (Table 2, Fig. 8). In addition, when the flood plain was mapped at a fine resolution (5 × 5 m quadrats), a significant number of tree-less quadrats were present (Figs. 3A–3C). Factors limiting the presence of trees were smaller in scale than the toposequence and were presumably spatially heterogeneous within the plains and flood plains. Juveniles of *D. tuberculatus* are more resistant to fire, compared with other deciduous dipterocarps (Nguyen *et al*., 2019), suggesting that spatial heterogeneity in fire intensity could be a limiting factor. As discussed in the previous paragraphs, low-intensity fire periods could be regularly expected where understory height and biomass were low (Figs. 3D–3E). On the other hand, a fire-free situation may occur more randomly, as suggested by the yearly variation in scattered unburnt areas with remaining forest floor vegetation (Figs. 3F–3H). The survival of juvenile trees may only be possible in areas where a fire-free or low-intensity fire period lasts by chance for a comparatively long interval.

Lower prevalence of trees or low understory height in the flood plain vs. stagnant water conditions

In some areas of the flood plain where understory height and biomass were low (Figs. 3D, 3E), low-intensity fire periods might be expected to continue. However, Group 3 was distributed in such areas (Fig. 7C) and tree-less quadrats were often present (Figs. 3A–3C). Another factor limiting the presence of trees may be stagnant water conditions. Water retention was observed during the rainy season in the flood plain of our study area, including outside of the flow path (authors, unpublished data). The occurrence of Cyperaceae species and *D. hookeri* in these areas (Fig. 3E) is suggestive of a stagnant water environment. Thus, such conditions during the rainy season could also serve as factors limiting the survival of tree seedlings.

Low recruitment of D. tuberculatus in Groups 2, 3 and 4 and S. obtusa in all groups vs. increase of fire events in recent years

We documented lower numbers of small-sized trees of *D. tuberculatus* and *S. obtusa* in Groups 2, 3, and 4 (Fig. 8A) and in all four groups (Fig. 8B), respectively. In investigating the regeneration of various types of deciduous dipterocarp forest in central Vietnam, Nguyen & Baker (2016) documented the absence of *S. siamensis* saplings and raised concerns about the future regeneration of forest types dominated by the species. Pin *et al*. (2013) suggested that lower numbers of small *D. tuberculatus* trees in Mondulkiri Protected Forest were associated with more frequent fires. Our findings suggest that recruitment of *D. tuberculatus* and *S. obtusa* has somehow been suppressed in recent years. Ghazoul *et al*. (1998) reported that the reproductive output of *S. siamensis* was not affected when population density was reduced from 96 to 62 flowering trees ha^{-1}, although it declined sharply when density was further reduced to 9 trees ha^{-1}. In our 4 ha study plot, the density of flowering dipterocarp trees was 85 trees ha^{-1} for *D. tuberculatus*, 34 trees ha^{-1} for *S. siamensis* and 32 trees ha^{-1} for *S. obtusa* (2014 census: Ito *et al*., 2016). This suggests that the low recruitment of dipterocarp species was unlikely to be due to a lack of flowering trees. However, if fire intensity has increased in recent years, new tree recruitment may have been inhibited. In surveying the deciduous dipterocarp forests of Stung Treng Province before the 1970s, Legris & Blasco (1972) did not observe lower numbers of small trees of the three species of dipterocarps, indicating that their recruitment was steadily progressing in the forest at that time. Climate-driven changes in drought and fire intensity in Southeast Asia may alter tree recruitment rates and cause long-term effects on the structure and species composition of deciduous dipterocarp forests (Nguyen *et al*., 2019). Fire intensity may also be changing due to alterations in the composition of forest floor vegetation and amount of biomass. Forest fires may lead to soil degradation, such as soil erosion (Sakurai *et al*., 1998) and nitrogen loss (Toda *et al*., 2007), which may lead to further changes in forest floor vegetation.

Future studies are necessary to verify the above hypotheses, particularly for the development of conservation plans. Identification of site characteristics along the toposequence and species-specific mechanisms that govern tree recruitment are urgent tasks for this study area.

Practical proposals for forest conservation

The most practical finding of our study is that the foot slopes and upper side of plains were topographical locations where the three dipterocarp species coexisted with many other tree species (Group 2, Table 2). The number of species in Group 2 was higher than in Group 4, although this difference was not statistically significant (Table 2) and Group 4 has relatively moderate species richness (Rundel, 1999). This result implies that the foot slopes and surrounding areas are densely stocked with mother trees of deciduous forest tree species and are a high priority for protection. Thus, to appropriately conserve deciduous dipterocarp forests, the overall toposequence must be maintained. This should include hills (Group 1) and flood plains or plains (Group 4), where typical forms of deciduous dipterocarp forests appear, as well as their foot-slope transition zones (Group 2).

In an applied context, understory height, which is more easily visible than soil type and thickness, may be useful as an indicator for spatial classification in conservation planning. For example, when implementing a reforestation project in a deforested area, *S. siamensis* will be unlikely to grow in areas other than hills. In addition, locations to plant *S. siamensis* may be determined by understory height during the rainy season.

The general homogeneity of the deciduous dipterocarp forests in Southeast Asia is partly because they are adapted to edaphically or topographically dry sites (Stott, 1990). The toposequence of landforms found in our 4 ha study plot had an elevational difference of 10 m for a horizontal distance of 200 m (Fig. 2D). Similar topographic gradients of environmental and forest properties at the same scale has been reported in undulating lands in peninsular Thailand (Ohkubo & Takeuchi, 1998). Our proposals for conservation can be applied to such toposequences of land forms, and the applicable area is expected to be considerably large.

Conclusions

We found clear spatial heterogeneity in vegetation at a scale of several hectares in Kratie Province, Cambodia. Strong associations of forest tree and forest floor vegetation with topographical properties were found along the toposequence. Various types of deciduous dipterocarp forests co-existed at this scale, although they were separated along the toposequence. We propose that along with the commonly limited forest types, the entire toposequence must be included in forest conservation efforts, because each type is established in an ecologically niche-differentiated manner along the toposequence. It is also crucial to determine the species-specific mechanisms governing tree distribution and such research will help to improve future forest conservation and reforestation projects.

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Annex 1 List of tree species occurring in the study plot

Khmer name: * provided by local informants. Status: D = dominant dipterocarps, A = associating non-dipterocarps, M = minor spp., E = evergreen spp.

Family / Species	Khmer Name *	Status	Tree density		Basal area		Max. DBH (cm)	No of trees in each group			
			stem ha^{-1}	%	m^2 ha^{-1}	%		1	2	3	4
Anacardiaceae											
Buchanania lanzan Spreng	KAPRAONG	A	14.00	2.52	0.211	1.53	31.4	16	15	7	18
Buchanania reticulata Hance	LEANG CHEY (sp. 1)	M	1.00	0.18	0.012	0.09	16.7	3	1		
Buchanania siamensis Miq.	LEANG CHEY (sp. 2)	M	1.75	0.32	0.049	0.36	26.8		5		2
Lannea coromandelica (Houtt.) Merr.	-	M	0.50	0.09	0.007	0.05	17.0				2
Bignoniaceae											
Heterophragma sulfureum Kurz	TA KUT TAMAT	A	6.25	1.13	0.075	0.55	35.3	8	14	1	2
Stereospermum cylindricum Pierre ex Dop	SANGKUOT THMAT	M	0.25	0.05	0.001	0.00	5.7			1	
Burseraceae											
Canarium subulatum Guill.	TALAT / * Pon Svar	M	0.25	0.05	0.002	0.02	10.3				1
Celastraceae											
Lophopetalum wallichii Kurz	* Ta Ley	M	3.75	0.68	0.096	0.7	34.0	1	11	2	1
Combretaceae											
Terminalia alata Heyne ex Roth [Glabrous type]	CHHLIK	A	76.00	13.68	1.82	13.22	38.5	153	127	12	12
Terminalia alata Heyne ex Roth [Hairy type]	CHHLIK	A	15.50	2.79	0.741	5.38	52.4		3	13	46
Terminalia chebula Retz var. chebula Retz	SRORMOR	A	7.00	1.26	0.277	2.01	39.9	5	4	5	14
Terminalia mucronata Craib & Hutch.	PRAM DOMLENG	M	4.00	0.72	0.221	1.60	49.4	1	2	3	10
Dilleniaceae											
Dillenia ovata Wall. ex Hook. f. & Thomson	LOWEY	M	1.75	0.32	0.012	0.08	14.0		2	1	4
Dipterocarpaceae											
Dipterocarpus tuberculatus Roxb.	KHLONG	D	106.25	19.13	4.235	30.77	52.8	81	139	121	84
Shorea obtusa Wall. ex Blume	PHCHEK	D	47.25	8.51	2.413	17.53	56.0	21	105	12	51
Shorea siamensis Miq.	RAING PHNOM	D	223.25	40.19	2.716	19.73	46.7	713	173	4	3
Ebenaceae											
Diospyros ehretioides Wall. ex G. Don	CHHOEU ROMEANG / LOMEANG	M	2.00	0.36	0.025	0.18	23.0		2		6
Diospyros pilosanthera Blanco var. helferi Bakh.	TROR YING	M (E)	0.25	0.05	0.008	0.06	20.1				1
Euphorbiaceae											
Aporosa octandra (Buch.-Ham. ex D. Don) Vickery	KRONG (sp. 1)	M	0.25	0.05	0.001	0.01	7.7	1			
Aporosa villosa (Lindl.) Baill.	KRONG (sp. 2)	M	0.75	0.14	0.009	0.07	19.0			3	
Bridelia retusa (L.) A.Juss.	CHHLIK PORK	M	0.25	0.05	0.001	0.01	6.4	1			
Guttiferae											
Garcinia cowa Roxb.	-	M	0.75	0.14	0.003	0.03	8.7		1		2

Annex 1 Cont'd

Family / Species	Khmer Name *	Status	Tree density		Basal area		Max. DBH (cm)	No of trees in each group			
			stem ha^{-1}	%	m^2 ha^{-1}	%		1	2	3	4
Lecythidaceae											
Careya arborea Roxb. / C. sphaerica Roxb.	KANNDOL	M	0.75	0.14	0.01	0.07	17.8	2	1		
Leguminosae											
Acacia harmanidiana (Pierre) Gagnep.	THMEAS TUK	M	0.25	0.05	0.011	0.08	23.5		1		
Dalbergia cochinchinensis Pierre	KRORNHOUNG	M	0.25	0.05	0.002	0.02	10.9		1		
Dalbergia cultrata Grah. ex Benth.	* Ta Meaek	M	2.00	0.36	0.036	0.26	21.5	3	4		1
Dalbergia nigrescens Kurz var. nigrescens	SNUOL	M	1.75	0.32	0.156	1.13	67.1		7		
Dalbergia oliveri Gamb. ex Prain	NEANG NOUN	M	0.25	0.05	0.005	0.04	15.9			1	
Pterocarpus macrocarpus Kurz	THNONG KRAHAM	M	0.75	0.14	0.017	0.12	28.6		1		2
Spatholobus parviflorus Kuntze	CHHAR / DORK CAV	M	0.75	0.14	0.005	0.03	9.5		2	1	
Xylia xylocarpa (Roxb.) W. Theob.	SOKROM	A	11.00	1.98	0.126	0.91	29.3	3	34	1	6
Loganiaceae											
Strychnos nux-blanda Hill	PRAVEK	M	2.25	0.41	0.015	0.11	15.4	1	4	1	3
Meliaceae											
Azadirachta indica A.Juss.	SDAO	M	0.25	0.05	0.001	0.00	5.7		1		
Myrtaceae											
Syzygium cumini (L.) Skeels	PRING BAI	M (E)	4.25	0.77	0.219	1.59	45.3		3	7	7
Opiliaceae											
Melientha suavis Pierre	* Pricch	M	0.50	0.09	0.003	0.02	9.5		2		
Phyllanthaceae											
Phyllanthus emblica L.	KANTOUT PREY	M	0.75	0.14	0.018	0.13	28.9		2	1	
Rubiaceae											
Catunaregam longispina (Roxb.) Tirveng	LVIENG SOR	M	3.00	0.54	0.015	0.11	11.9	5	6		1
Catunaregam tomentosa (Bl. ex. DC.) Tirv.	LVIENG KROHOM	M	0.25	0.05	0.003	0.02	12.3				1
Gardenia obtusifolia Roxb.	BAKDORNG	M	4.50	0.81	0.014	0.10	8.8	14	2	1	1
Mitragyna rotundifolia (Roxb.) O.K.	KHTOM / KHTOM PHNOM	A	5.75	1.04	0.107	0.78	23.5	2	13	2	6
Morinda coreia Ham.	NHOR	M	1.00	0.18	0.021	0.15	29.6	2			2
Neonauclea sessilifolia Merr.	ROLEAY	M	0.25	0.05	0.03	0.21	38.8			1	
Pavetta tomentosa Roxb. ex Sm.	PREAH CHHNET / PUK CHHMAR	M	0.25	0.05	0.001	0.00	5.4	1			
Sapotaceae											
Madhuca stipulacea Fletcher	SRAKUM	M (E)	1.00	0.18	0.007	0.05	13.8	2	1	1	
Tiliaceae											
Grewia eriocarpa Juss.	PO PLEAR	M	0.25	0.05	0.001	0.01	8.2	1			

Annex 1 Cont'd

Family / Species	Khmer Name *	Status	Tree density		Basal area		Max. DBH (cm)	No of trees in each group			
			stem ha^{-1}	%	m^2 ha^{-1}	%		1	2	3	4
Verbenaceae											
Vitex pinnata L.	POPOUL	M	0.50	0.09	0.009	0.07	16.0	1		1	
		Total	555.50	100	13.76	100	67.1	1041	689	203	289

Annex 2 Aboveground understorey biomass in the study plot

Location		Aboveground understorey biomass (Mg/ha)									
x	y	Total	*Vietnamosasa pusilla*	Other Gramineae	Cyperaceae	*Dillenia hookeri*	Fabaceae	*Shorea obtusa*	*Shorea siamensis*	Other shrubs & herbs	Remarks (emerging species)
200	200	4.75	4.42				0.27			0.06	Asteraceae
150	200	4.47	1.41	2.43						0.64	Liliaceae
100	200	1.60	0.07	1.42						0.11	Herb
50	200	3.09		1.60				1.49			
0	200	1.14	1.09		0.02		0.02			0.02	
0	150	2.32	1.99		0.09					0.24	*Heterophragma sulfureum* Kurz, *Vitex*
50	150	5.04			0.28	4.77					
100	150	2.13	0.89	1.18						0.06	
150	150	3.48	2.98	0.16			0.27			0.07	Schizaeaceae
200	150	4.64	4.62	0.02						0.00	Dioscoreaceae
200	100	2.95		0.56					2.39		
150	100	4.07	4.07								
50	100	4.36	3.84	0.18			0.35				
0	100	6.98	6.95	0.01			0.00			0.02	Liliaceae
0	50	7.17	7.10						0.03	0.04	Vitex sp.
50	50	4.28	4.23	0.05			0.00				
100	50	6.20	6.20								
150	50	3.68							3.68		
200	50	1.53	0.33	1.06			0.02			0.11	
200	0	4.23		4.14			0.01			0.08	Asteraceae
150	0	1.23		1.22						0.01	

Annex 2 Cont'd

Location		Aboveground understorey biomass (Mg/ha)									
x	y	Total	*Vietnamosasa pusilla*	Other Gramineae	Cyperaceae	*Dillenia hookeri*	Fabaceae	*Shorea obtusa*	*Shorea siamensis*	Other shrubs & herbs	Remarks (emerging species)
100	0	2.10		2.08						0.02	
50	0	2.12		2.10						0.01	
0	0	2.62		2.19		0.14				0.29	Malvaceae

A dry season glimpse of watersnake bycatch and trade from the flooded forests of Kampong Khleang, Tonlé Sap Lake

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មូលន័យសង្ខេប

បឹងទន្លេសាប គឺជាប្រព័ន្ធអេកូឡូស៊ីដ៏សម្បូរបែបមួយ ទោះបីជាប្រភេទសត្វទឹកជាច្រើនត្រូវបានថយចុះ ដោយសារតែការប្រមូលផលច្រើនលើសលុបក៏ដោយ។ យើងបានធ្វើការវាយតម្លៃលើបរិមាណ និងសមាសភាពនៃពស់ទឹកដែលចាប់បានដោយចៃដន្យដោយអ្នកនេសាទ តាមរយៈការពិនិត្យឯកត្តៈនីមួយៗដែលជាផលចាប់របស់អ្នកនេសាទ និងដាក់លក់ប្រចាំថ្ងៃដោយអ្នកជំនួញ ក្នុងរយៈពេល ១០ថ្ងៃ ក្នុងស្រុកកំពង់ឃ្លាំង នៅខែវិច្ឆិកា ឆ្នាំ២០១៩។ ប្រវែងនិងទម្ងន់នៃសំណាកនីមួយៗ ព្រមទាំងប្រេកង់នៃការកើតឡើង (frequency of occurrence) នៃប្រភេទពស់នីមួយៗត្រូវបានកត់ត្រា។ អ្នកនេសាទចំនួន២១នាក់ និងអ្នកភូមិជាច្រើននាក់ផ្សេងទៀតត្រូវបានសម្ភាសន៍ដើម្បីស៊ើបអង្កេតបន្ថែមទៀតពីបរិមាណ និងនានាភាពនៃពស់ទឹកចាប់បានដោយចៃដន្យ វិធីសាស្ត្រចាប់ ពេល និងទីតាំងនៃការបន្តពូជ និងការប្រើប្រាស់ផ្សេងៗទៀត។ ពស់ទឹក៨ប្រភេទត្រូវបានកត់ត្រា ប្រភេទដែលមានច្រើនជាងគេក្នុងគំរូតាងនៃទិន្នផលនេសាទ និងពស់ដែលដាក់លក់ គឺពស់ព្រលិតដូង [Tonle Sap watersnake (*E. longicauda*)] (*n*=763) និងពស់ព្រលិត [rainbow watersnake (*E. enhydris*)] (*n*=209)។ តាមរយៈការសម្ភាសន៍បានបង្ហាញថា ទិន្នផលពស់ទឹកដែលចាប់បានដោយចៃដន្យខ្ពស់បំផុតមានពីរដងក្នុងមួយឆ្នាំ គឺនៅរដូវបន្តពូជ។ ដោយពស់ទឹកទន្លេសាបជាប្រភេទដែលរងគ្រោះជាសាកល (*globally Vulnerable)* និងមានលក្ខណៈដោយឡែកសម្រាប់បឹង យើងស្នើឲ្យមានការស្រាវជ្រាវបន្តទៀតដើម្បីស្វែងយល់ពីបម្រែបម្រួលផលចាប់ និងជំនួញទៅតាមពេល និងទីតាំង ក៏ដូចជាផលចាប់ដោយចេតនា ដើម្បីកំណត់ការរឹតបន្តឹង ការពារប៉ូពុយឡាស្យុងពស់ទឹកនៅក្នុងតំបន់ ជាពិសេសក្នុងរដូវបន្តពូជ។

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Abstract

The Tonlé Sap Lake is a rich ecosystem although many of its aquatic species have been depleted by overharvesting. We assessed the quantity and composition of watersnakes unintentionally caught during routine fishing practices by examining individuals in the bycatch of a fisherman and sold by a snake trader each day for ten days in Kampong Khleang Commune in November 2019. The length and mass of each specimen and frequency of occurrence of each species was recorded. Twenty-one fishermen and other villagers were interviewed to further investigate the volume and variety of watersnakes caught as bycatch, methods of capture, timing and location of breeding and subsequent uses of snakes. Eight species of watersnake were recorded. The species most commonly reported and most abundant in our bycatch and trader samples were the Tonlé Sap watersnake *Enhydris longicauda* (*n*=763) and the rainbow watersnake *E. enhydris* (*n*=209). Interviews revealed that watersnake bycatch was highest at two times of the year which coincided with their breeding seasons. As the Tonlé Sap watersnake is globally Vulnerable and endemic to the lake, we recommend further research into spatial and temporal variation in bycatch and trade, as well as intentional harvesting, to determine if restrictions are warranted to safeguard local watersnake populations, particularly during the breeding season.

Keywords Bycatch, Cambodia, Kampong Khleang, Tonlé Sap Lake, watersnakes.

Introduction

Squamate reptiles are often under-represented in conservation initiatives (Beaupre & Douglas, 2009; Tingley *et al*., 2016) with around 15% of species being classified as Data Deficient by the IUCN Red List of Threatened Species and 16% threatened with extinction (IUCN, 2021). Snakes serve as a source of food for other predators and they regulate the populations of their prey species. Their use of multiple habitats for feeding, hibernation and reproduction means that major changes to snake populations may be an early sign of habitat degradation, associated effects of climate change, and other alterations (Beaupre & Douglas, 2009).

The Tonlé Sap Lake, in the centre of Cambodia, is the largest freshwater lake in Southeast Asia. The lake is unique for its flood pulse ecosystem which causes it to expand from 2,600 km^2 in the dry season to 15,000 km^2 during the peak of the wet season (Arias *et al*., 2014a). This creates a seasonally flooded forest near the margins of the lake which serves as a breeding ground for fish and other aquatic life including watersnakes (Campbell *et al*., 2006). As a result of decreases in annual rainfall in Cambodia since 1951, the seasonality of the lake has become more irregular (Thoeun, 2015). The construction of dams along the Mekong and the effects of irrigation and water use for agricultural purposes have also modified the hydrology of the lake (Evans *et al*., 2005; Arias *et al*., 2014b). The dams regulate water flow from the Mekong River and reduce the water entering the lake during the flood pulse. These changes have a detrimental effect on the wildlife of the lake that may delay their breeding and migration to match the increase in rain and rising water levels (Campbell *et al*., 2006).

Fish comprise 70% of the protein intake of Cambodian people, most of which is sourced from the lake. In the past, many of the fishing grounds in Tonlé Sap Lake were contained within commercial fishing lots, but these have since been replaced with communal use zones (Cooperman *et al*., 2012). Unfortunately, this has led to communities over-exploiting the natural resources of the lake and depleting populations of fish (Kuenzer, 2013). Residents of the lake have raised crocodiles since the 1940's including pure species and hybrids of the native Siamese crocodile (*Crocodylus siamensis*) and saltwater crocodile (*C. porosus*) to supplement their livelihoods. Since the 1990's, the Cuban crocodile (*C. rhombifer*) has also been imported (Targarona *et al*., 2008; Daltry *et al*., 2016). This has resulted in a need for low-cost crocodile food with many people having turned to watersnakes as a means to meeting this demand (Brooks *et al*., 2010). Watersnakes are often caught as bycatch along with fish, making them an easy supplement for crocodile food when fish are in short supply (Stuart *et al*., 2000; Brooks *et al*., 2007). In addition, in recent years, watersnakes have begun to be consumed by people who live around the lake and in other parts of Cambodia (Brooks *et al*., 2007).

Seven watersnake species are commonly caught in the Tonlé Sap Lake (Brooks *et al*., 2009). Most are homalopsids, with the rainbow watersnake (*Enhydris enhydris*) dominating the catch (Stuart *et al*., 2000; Brooks *et al*., 2009). Rainbow watersnakes are widespread across Southeast Asia and are easily mistaken for the closely related Mekong mudsnake (*E. subtaeniata*). Most of the watersnakes caught in the lake eat primarily fish except for the semi-aquatic yellow-spotted keelback (*Fowlea flavipunctatus*) which mostly eats large frogs, and the red-tailed pipe snake (*Cylindrophis ruffus*) which preys on snakes and eels (Brooks *et al*., 2009). The Tonlé Sap watersnake (*E. longicauda*) is the only snake species endemic to the Tonlé Sap Lake and is categorized as Vulnerable (Murphy *et al*., 2010). All of these species are commonly found in the trade in aquatic snakes from the Tonlé Sap although less commonly than *E. enhydris* (Stuart *et al*., 2000; Brooks *et al*., 2007). Other common snake species found in the trade include the banded swamp snake (*Homalopsis buccata*), Bocourt's watersnake (*Subsessor bocourti*) and the tentacled snake (*Erpeton tentaculatum*). *Homalopsis buccata* and *S. bocourti* are particularly desirable for snake traders because the skins can be sold in foreign markets for clothing and accessories (Lieng *et al*., 2010). Very little is known about the ecology of most snake species in the lake and no published data are available on their preferred habitat types or movement patterns.

Over 770 tons of snakes (roughly 6.9 million individuals) were traded annually from the Tonlé Sap Lake between 2004–2005 (Brooks *et al*., 2007). This is the largest watersnake trade in the world. The snakes are used primarily as crocodile food but are also traded for their skins and human consumption. Watersnakes can be dried and sold as food for prices that are comparable to those of fish (Chhut, 2018). *Enhydris enhydris* comprises two-thirds to three-quarters of the trade and *E. longicauda* is the second most common species, accounting for roughly 10% of the trade (Brooks *et al*., 2007). These figures are similar to results from a foundational study on homalopsid trade in Tonle Sap, which found that *E. enhydris* comprised 80% of 3,000–4,000 snakes harvested in 1999–2000 (Stuart *et al*., 2000). The trade follows seasonal trends and peaks near the beginning and at the end of the wet season (June–October) when water starts to enter and then recede from the lake. This coincides with the beginning of snake breeding season which occurs at the onset of the wet season. Overharvesting has caused severe decline in snake populations (Brooks *et al*., 2007). Most species have slow growth cycles and late maturity which do not allow their populations to recover if they are heavily exploited (Brooks *et al*., 2007).

The aim of our study was to assess the diversity, abundance and sizes (mass and length) of watersnake species caught as bycatch and traded during the dry season at Chamkar Youn village in Kampong Khleang Commune, Siem Reap Province, Cambodia. Despite this being a short-term study in one location, we were interested to determine if species composition and sizes had changed since those found in earlier studies (Brooks *et al*., 2009).

Methods

Our data collection took place in Chamkar Youn village in Kampong Khleang Commune near the northern edge of the Tonlé Sap Lake (13°06.204′N, 104°07.478′E) for ten days in November 2019. The village is located in the floodplain of the lake and is heavily influenced by the flood pulse. The flooded forest nearby allows locals to catch a wide range of fish and watersnake species at different life stages. Watersnakes and fish lay their eggs or give birth to live young in the flooded forest (Campbell *et al*., 2006).

We employed two approaches in data collection. The first was to quantify watersnake bycatch of a local fisherman, as well as the composition of species sold by a local snake trader. Secondly, to supplement our observations we interviewed fishermen and other local villagers to understand the volume and species diversity of watersnakes caught as bycatch, their habitats, common capture methods, the timing and location of breeding, and their subsequent uses.

Some of our watersnake specimens came from the same fisherman who provided access to his catch each day for ten days. The fisherman used a trap known as a "lop" to collect fish, trapping watersnakes as bycatch (Fig. 1). Each specimen was weighed in grams and measured for snout-vent length (SVL, in cm) to calculate the minimum, maximum and mean mass and body length for each species. We also counted and weighed watersnakes sold at the local market by one snake trader each day. A total count of each species was recorded. We then compared our results to the means reported by Brooks *et al*. (2009) using 2-tailed *t*-tests. Due to time constraints, we opted to focus on one fisherman and one trader for this section of the study to get an accurate overview over time of their individual activity.

Interviews were semi-structured and aimed to develop our understanding of which species are caught, their habitats, capture methods, the timing and location of breeding, and their use. The questions were translated into Khmer by a graduate translator from the Royal University of Phnom Penh. Respondents were selected using key informant (Marshall, 1996), snowball, convenience and random sampling methods (Miller & Brewer, 2003). A total of 21 fishermen, watersnake traders and other local villagers were interviewed. To assist the interviewees and verify their reliability, we showed pictures of snakes common in the lake and some non-native or non-aquatic species (e.g., *Boiga siamensis* and *B. cyanea*) to determine if the interviewees were genuinely able to recognise species from the lake.

Fig. 1 "Lop" trap used by many fishermen in Kampong Khleang Commune, Cambodia.

Table 1 Snout to vent length and mass of watersnake species recorded in bycatch and trade in Kampong Khleang Commune, along with values reported for females (f) and males (m) by Brooks *et al*. (2009). Figures for bycatch and trade are given as min–max, mean ± standard error (*n*), and mean ± standard error (*n*) for Brooks *et al*. (2009).

Species	Snout to Vent Length (cm)		Mass (g)		
	Bycatch	Brooks *et al*. (2009)	Bycatch	Trade	Brooks *et al*. (2009)
Acrochordus granulatus	26.9 (1)	-	11.0 (1)	-	-
Enhydris enhydris	28.4–72.0, 42.8 ±0.9 (77)	50.5 ±1.2 (f) 47.6 ±0.1 (m) (4197)	17.0–216.0, 65.19 ±4.18 (77)	14.0–178.0, 59.53 ±3.07 (132)	97.8 ±1.2 (f) 81.5 ±0.5 (m) (3602)
Enhydris longicauda	24.9–61.0, 38.9 ±0.4 (228)	48.9 ±0.2 (f) 44.2 ±0.2 (m) (1602)	20.0–310.0, 82.33 ±2.37 (228)	17.0–243.0, 87.07 ±1.79 (534)	150.9 ±2.6 (f) 117.5 ±4.6 (m) (1617)
Cylindrophis ruffus	39.0–69.4, 57.6 ±9.2 (3)	71.5 ±0.8 (f) 68.6 ±1.2 (m) (115)	177.0–300.0, 220.67 ±39.73 (3)	-	224.4 ±8.0 (f) 220.9 ±10.5 (m) (127)
Homalopsis buccata	41.6–42.2, 41.9 ±0.3 (2)	74.0 ±0.5 (f,m) (1573)	57.0–77.0, 67.0 ±10.0 (2)	73.0 (1)	242.2 ±5.5 (f) 249.8 ±3.8 (m) (1452)
Erpeton tentaculatum	42.5–57.0, 49.6 ±1.4 (10)	50.1 ±0.3 (f) 45.9 ±0.2 (m) (746)	83.0–217.0, 132.90 ±15.20 (10)	292.0 (1)	104.1 ±2.3 (f) 81.8 ±1.3 (m) (766)
Fowlea flavipunctatus	33.7–78.8, 49.8 ±3.18 (18)	-	34.0–356.0, 126.94 ±24.68 (18)	74.0 (1)	-
Subsessor bocourti	28.9–84.0, 43.9 ±5.3 (11)	57.3 ± 2.6 (f) 53.2 ±1.7 (m) (141)	44.0–473.0, 143.27 ±41.36 (11)	41.0–287.0, 116.11 ±15.05 (27)	267.9 ±31.8 (f) 196.9 ±14.7 (m) (136)

Results

Data from a total of 87.94 kg and 1,046 watersnake specimens was collected over our ten-day study period. Three hundred and fifty of these snakes were caught by one local fisherman as bycatch and 696 were being sold by one local snake trader. Eight species were caught by the fisherman including *E. longicauda* (*n*=228), *E. enhydris* (*n*=77), *E. tentaculatum* (*n*=10), *S. bocourti* (*n*=11), *F. flavipunctatus* (*n*=18), *H. buccata*, *C. ruffus* and *Acrochorhus granulatus* (*n*=<5 apiece). The fisherman's bycatch yielded a mean of 3.01 kg (SE ± 0.18) of watersnakes per day. The mean SVL and mass for each species were calculated from this daily catch (Table 1).

Data collected from the watersnake trader showed that 9.7 kg of snakes were bought by the trader to sell per day on average (SE±1.73). Similar to the fisherman's catch, *E. longicauda* was the most common species bought by the snake trader (*n*=534). The total number of other snakes the seller received included *E. enhydris* (*n*=132) and *S. bocourti* (*n*=27). There was only one specimen of each of the three remaining species (Table 1).

The mean mass of species with larger sample sizes from the fisherman and trader (*E. enhydris*, *E. longicauda* and *S. bocourti*) appeared to be less than values reported in 2009: *E. enhydris* (fisherman= 65.19 ± 1.48 g, trader= 59.53 ± 3.07 g, Brooks *et al.*, 2009= 97.8 ± 1.2 g (females) and 81.5 ± 0.5 g (males)), *E. longicauda* (fisherman= 82.33 ± 2.37 g, trader= 87.07 ± 1.79 g, Brooks *et al.*, 2009= 150.9 ± 2.6 g (females) and 117.5 ± 4.6 g (males)), and *S. bocourti* (fisherman= 143.27 ± 41.36 g, trader= 116.11 ± 15.05 g and Brooks *et al.*, 2009= 267.9 ± 31.8 g (females) and 196.9 ± 14.7 g (males)) (Table 1). However, there were no significant differences between our data and the means reported for male or female snakes by Brooks *et al.* (2009) (p=>0.05). The same was true for mean SVL measurements.

Eleven of the 21 respondents we interviewed reported catching watersnakes as bycatch. Five respondents reported buying snakes from market sellers for personal consumption and two reported they bought them for crocodile food. The remaining three respondents reported that they exclusively caught fish and did not purchase watersnakes for consumption. Our interviewees also included two crocodile farmers, one of whom indicated that they purchased 300–400 kg of snakes each week to feed ca. 100 crocodiles. In contrast, the other farmer said they bought ca. 30 kg each week to feed ca. 50 crocodiles.

Sixteen respondents claimed the lop (Fig. 1) was their fishing tool when they unintentionally caught watersnakes and eight of these said it was used in addition to a gillnet. Only two respondents said they exclusively used a gillnet. Three respondents were able to indicate locations where watersnakes were more abundant and claimed they caught more in shallower areas of the lake near the flooded forest. Four of the 21 respondents (19%) reported watersnakes in their catch were smaller compared to the past, whereas eight (38%) reported no change in size. The remainder were unsure.

Consistent with our quantitative data, all respondents indicated that *E. enhydris* and *E. longicauda* were the most common species caught (Fig. 2), followed by *Xenochrophis piscator*, despite none of the latter being recorded in our bycatch and trade samples.

Most respondents said more snakes were caught during the months of June and July (wet season) as well as November and December (Fig. 3). These months were also reported as the period when respondents found eggs in the snake oviduct.

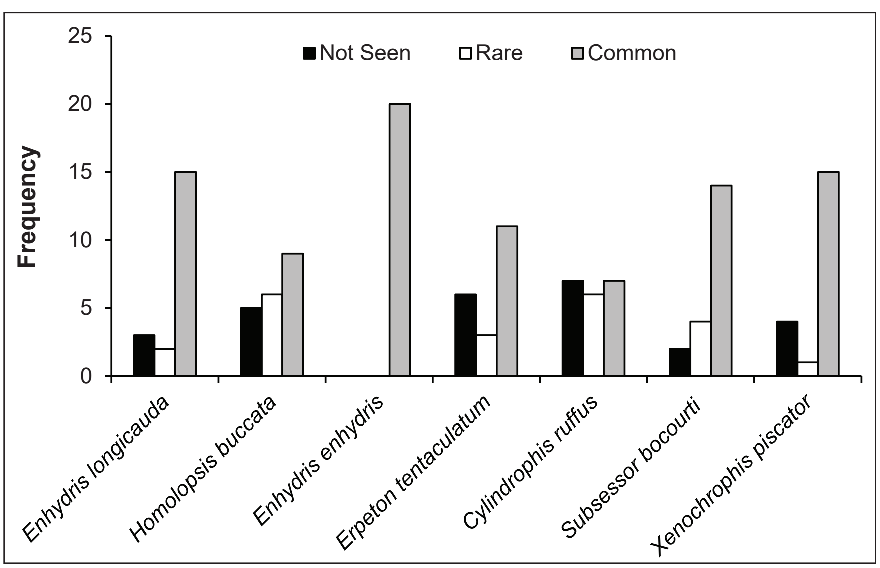

Fig. 2 Frequency of reports from 21 respondents on different watersnake species as common, rare, or not seen in Kampong Khleang Commune, Cambodia.

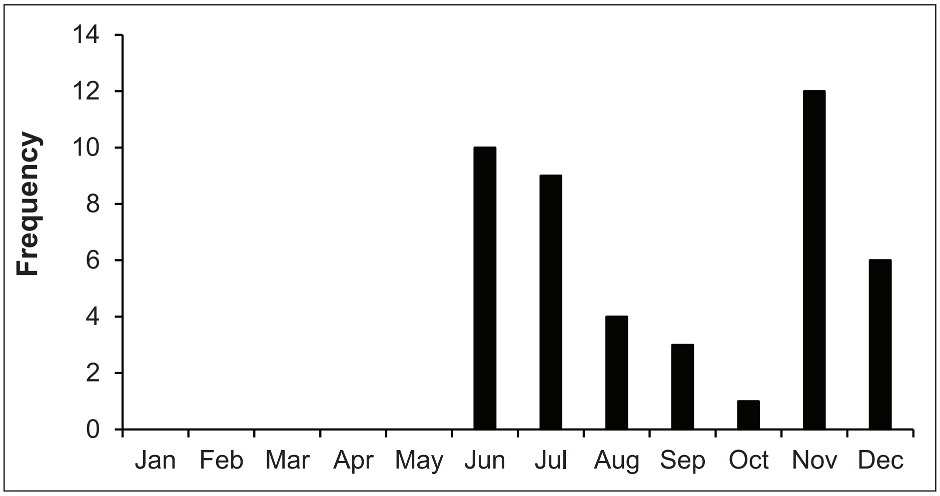

Fig. 3 Frequency of reports from 21 respondents on months when greater numbers of watersnakes are present in fish catches in Kampong Khleang Commune, Cambodia.

Discussion

Our short study found that *E. longicauda* was more abundant than *E. enhydris* in samples from the snake trader and bycatch. The former species accounted for 77% of the trader's collection and 65% of the bycatch. This differs from previous studies which found *E. enhydris* was the most common watersnake caught (Stuart *et al*., 2000; Brooks *et al*., 2007). Despite earlier studies being more extensive, our results offer a glimpse that suggests three possible scenarios: a decrease in the *E. enhydris* population which could be related to harvesting for crocodile food or human consumption; an increase in the *E. longicauda* population; or greater proportions of *E. longicauda* being caught due to the use of lops rather than gillnets as the main capture method. Further studies comparing temporal and spatial variations and catch techniques are required. The fact that *E. longicauda* was the most commonly caught species in our study is a cause for concern because the species is endemic to the waters and surrounding wetlands of Tonlé Sap Lake and listed as Vulnerable by the IUCN (Murphy *et al*., 2010). If these trends continue unabated by any of kind restrictions, the quantities harvested could place major stress on local populations of the species and increase their risk of extinction.

Although the average mass of some watersnake species in our study appeared to be lower than previous reports (Table 1), the differences were not statistically significant. Since our sample size was much smaller than Brooks *et al*. (2009), this may have affected the reliability of our comparison. If future studies with a larger sample size were to show significant differences however, it is possible that over-fishing at the Tonlé Sap Lake could have altered the reproductive ecology of *E. enhydris* (Murphy *et al*., 2002). It is necessary to consider that many of the large, mature and fecund individuals might be captured and removed from the lake at increased rates, leaving only younger and smaller snakes behind. As such, continuation and expansion of our study during the wet season might provide more information on the mass and length of more fully-grown snakes and reduce the number of juveniles collected.

Because many of our respondents indicated that the lop was the primary tool used for fishing—a generalized trap traditionally used to catch fish which does not specifically target snakes—this could have implications for any future attempts to regulate the capture of watersnakes (Deap *et al*., 2003). Additionally, it is possible that people on the lake use an alternative means of catching snakes that we did not learn about; for example, the use of illegal fishing equipment. Moreover, the use of the lop may have skewed our results towards the types and sizes of watersnakes caught.

Although some of our respondents claimed they only caught fish and never buy or sell watersnakes, all of them were able to distinguish the different species and often provided their Khmer names. Even people who claimed to have limited interactions with watersnakes recognized and named at least some of the species displayed in photographs. Additionally, the species that most respondents identified as common matched those most often found in the samples we examined from the individual fisherman and trader. Some respondents also identified the rarer and more expensive species such as *S. bocourti*.

Our interview data regarding the seasonality of snakes and their eggs were fairly consistent. The periods that respondents claimed most snakes were caught coincided with those when they claimed eggs were found in the oviduct or when more snakes than normal were present. June and July were identified as the months of greatest snake abundance and this period also marks the onset of rising water levels in the lake during the flood pulse (Kummu *et al*., 2008). This observation is consistent with reports that *E. enhydris* has two breeding seasons (in April/May and November), whereas the other species only enter vitellogenesis in November and December (Murphy *et al*., 2002; Brooks *et al*., 2009). This corresponds with villager reports that more watersnakes are caught in the flooded forest in June and July where they give birth to live young. November and December were also commonly identified as months when more snakes were caught, which aligns with the snakes following the water's edge for refuge during the dry season (Brooks *et al*., 2007).

Previous studies have indicated that crocodile farms are the main destination of watersnakes caught in the Tonlé Sap Lake (Brooks *et al*., 2008, 2010). However, most of our respondents indicated that snakes are mostly used for human consumption. One of the crocodile farmers we interviewed also claimed that only three large crocodile farms existed near the lake, thus accounting for a relatively small portion of snake harvests and sales conducted in the region. However, our respondents did not refer to the hundreds of smaller farms located in the region (Daltry *et al*., 2016). While it was claimed that the larger crocodile farms might consume upwards of 300 kg of watersnakes per week, 10 of 21 respondents reported buying or selling watersnakes for human consumption. This shift may have consequences for watersnake populations and families living on the lake. The crocodile farmers we interviewed indicated that prices for snakes were much lower in the past and that they now bought fewer snakes for their crocodiles due to their higher costs. Previous research has suggested that the price of snakes has increased with the price of fish regardless of their abundance (Brooks *et al*., 2010; Chhut, 2018) and most of our respondents reported prices of 2.50–3.00 USD per kg for *E. longicauda* and *E. enhydris*. They also attributed the price increase to the growing popularity of snakes for human consumption.

Although we did not explore potential drivers of the increased popularity of watersnakes for human consumption, the decreasing abundance of fish in the lake could be one reason for this (Brooks *et al*., 2007; Campbell *et al*., 2006; Kuenzer, 2013). As the traditional food source (fish) decreases for people living on the lake, more people could turn to snakes to supplement their protein intake. Outside demand could represent another reason. Several respondents claimed that outsiders often came to the village to purchase watersnakes. While they did not indicate how many were bought and for what purpose, it is possible these are sold in the restaurant trade or street stalls in nearby Siem Reap and Phnom Penh.

Regular monitoring of watersnake populations in the Tonlé Sap ecosystem is important because Cambodians increasingly rely on them for food. This would also enable early recognition of population changes which could prevent negative impacts on the ecology of the lake if populations were to decline. Watersnakes serve as an important food source for a variety of bird species (Beaupre & Douglas, 2009), many of which are endemic and/or endangered. The watersnake populations themselves are also experiencing a decrease in their food supply as increasing amounts of fish are being taken from the lake (Campbell *et al*., 2006; Brooks *et al*., 2007; Kuenzer, 2013). The loss of their prey, combined with unmonitored harvesting from the lake and habitat degradation, could put some or all watersnake species in the lake at greater risk, along with the wildlife that depend on them for food.

While the findings we report are factual, these do have some limitations. For example, as our data collection was confined to a ten-day period, we were unable to identify seasonal trends that could have influenced our results. Further, since many of our study respondents indicated that our study took place during the peak snake season, our results regarding the quantity of snakes caught are probably not indicative of snake catches throughout the year but rather an over-estimate of yearly means. Further studies focusing on temporal variation in catches are required to report on this conclusively. Additionally, we trusted that our study respondents were honest in claiming that they caught watersnakes unintentionally, but this might not have been the case in every instance.

Our small sample size and inclusion of data from only one snake trader and fisherman also makes it difficult to generalize our findings. We cannot be sure that the data from our study village are representative of other villages found on the Tonlé Sap Lake and therefore recommend that future studies incorporate multiple study sites and fishermen utilizing various fishing techniques to facilitate direct comparisons with earlier studies. We also cannot be certain if the fisherman and snake trader we interviewed provided access to all the snakes they had each day. Because of our limited study period and potential biases associated with our sampling techniques, further research is needed to confirm our results and generalize these to the wider Tonlé Sap region. Despite its limitations however, the fact that our data consistently indicates that the species caught most often is both endemic and Vulnerable suggests that a similar pattern could be emerging on a broader scale.

Overall, our results suggest that continuation of watersnake harvesting at current levels is unlikely to be sustainable. Because the times of year when watersnake catches are greatest coincides with their breeding seasons, this could lead to further population decreases which they may not recover from. We therefore recommend restriction of watersnake harvests during the breeding season to safeguard population recruitment. In line with previous studies (Murphy *et al*., 2002; Brooks *et al*., 2009), it would also be beneficial to restrict the capture of large, fecund females. Education of local people on the species currently threatened and creation and monitoring of more monitored conservation zones in the flooded forest would also help to reduce overharvesting of vulnerable species. Consideration of a national action plan for *E. longicauda* is also warranted, as is research evaluating the impact of crocodile farms and restaurant trade on the species. While *E. longicauda* populations still appear to be relatively abundant, establishment of an insurance population and studies to improve understanding of its behaviour and ecology are advisable considering the species is not only endemic and Vulnerable but increasingly consumed by people. Ultimately, should current harvests and trade levels continue or expand in future, the extinction risk for species such as *E. longicauda* will likely increase.

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The use of non-invasive sampling to estimate long-term abundance of *Hippocampus kuda* in the Koh Sdach Archipelago, Cambodia

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មូលន័យសង្ខេប

ប្រជុំកោះស្ដេចត្រូវបានរៀបចំជាទីតាំងបន្ទាប់ សម្រាប់ដាក់ជាតំបន់គ្រប់គ្រងជលផលសមុទ្រនៅប្រទេសកម្ពុជា។ នៅពេលដែលការប្រកាសខិតជិតមកដល់ វាចាំបាច់ណាស់ក្នុងការកំណត់អត្តសញ្ញាណប្រភេទជីវៈចម្រុះក្នុងសមុទ្រដែលកំពុងរងការគំរាមកំហែង ដើម្បីជាមូលដ្ឋានក្នុងការកំណត់តំបន់គ្រប់គ្រងនៅក្នុងប្រជុំកោះនេះ។ ទោះយើងដឹងហើយថាប្រជាជនកម្ពុជាភាគច្រើនពឹងផ្អែកលើវិស័យជលផលដើម្បីបម្រើដល់សន្តិសុខស្បៀង និងជាប្រភពប្រាក់ចំណូលមូលដ្ឋានក៏ដោយ ក៏ការសិក្សាស្រាវជ្រាវអំពីសមុទ្រ ដើម្បីជួយដល់ការអភិរក្សសមុទ្រប្រកបដោយប្រសិទ្ធភាពនៅតែមានភាពខ្វះខាត។ ចាប់ពីឆ្នាំ២០១៤ ដល់ ២០២១ យើងបានធ្វើការតាមដាននៅតាមទីតាំងសិក្សាចំនួនប្រាំកន្លែងនៅក្នុងប្រជុំកោះនេះ ដើម្បីសង្កេតពីនិន្នាការប៉ូពុយឡាស្យុងនៃសត្វសេះសមុទ្រ *Hippocampus kuda* (Teleostei: Syngnathidae) ដែលត្រូវបានគេដកហូតលើសកម្រិតតាមរយៈការកំណត់ជាប្រភេទដែលត្រូវប្រមូល ការមិនបានកំណត់ប្រភេទឧបករណ៍នេសាទជាក់លាក់ និងការបាត់បង់ទីជម្រក។ យើងបានរកឃើញថា ដង់ស៊ីតេទូទៅនៃប្រភេទសត្វនេះមានកម្រិតទាប (0.000៨ SE ±0.000១ ឯកត្តៈ/ម²) ហើយមិនមានភាពខុសគ្នាពីកន្លែងមួយទៅកន្លែងមួយទេ។ ភាពលប់របស់វាហាក់ដូចជានៅថេរដោយមិនមានការផ្លាស់ប្ដូរគួរឱ្យកត់សម្គាល់ទេក្នុងអំឡុងពេលសិក្សា។ យើងបានកំណត់ទីតាំងសិក្សាដែលមានលក្ខណៈបរិស្ថានផ្សេងៗគ្នា ចាប់ពីតំបន់មានខ្សាច់ទទេ រហូតដល់វាលស្មៅសមុទ្រ ហើយការសិក្សានេះបង្ហាញថា *H. kuda* អាចសម្របខ្លួនបានខ្ពស់ ជាពិសេសអាចរស់នៅនិងប្រើប្រាស់ទីជម្រកទូទៅជុំវិញខ្លួនបាន ហើយក៏អាចបម្លាស់ទីទៅកាន់តំបន់ដែលវាចូលចិត្តផងដែរ។ នេះបង្ហាញពីសក្តានុពលនៃភាពធន់របស់ប៉ូពុយឡាស្យុងនៃប្រភេទ ធៀបនឹងប្រភេទសត្វដែលមានតម្រូវការទីជម្រកជាក់លាក់។ ការសិក្សាស្រាវជ្រាវអំពីបម្រែបម្រួលដង់ស៊ីតេនៃប៉ូពុយឡាស្យុងតាមរដូវកាល គឺចាំបាច់ដើម្បីកំណត់ពីនិន្នាការបម្រែបម្រួលព្រមទាំងអថេរមួយចំនួនទៀតដូចជាគុណភាពទឹក និងជម្រើសនៃទម្ររ ត្រូវតែមានការសិក្សាបន្ថែមទៀតដើម្បីស្វែងយល់អំពីទំនោរនៃការប្រើប្រាស់ជម្រករបស់សេះសមុទ្រ *H. kuda* នៅប្រជុំកោះស្ដេច។

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Abstract

The Koh Sdach Archipelago has been designated as the next location for a marine fisheries management area in Cambodia. As the final phase of the proclamation draws near, it is essential to identify threatened populations of marine species to guide the design of appropriate zones for different forms of management within the archipelago. Despite much of Cambodia's population being reliant upon the fisheries industry for food security and primary income, there is a paucity of marine research to facilitate effective conservation. We undertook monitoring at five sites in the archipelago between 2014 and 2021 to investigate population trends of *Hippocampus kuda* (Teleostei: Syngnathidae), a heavily exploited seahorse species which is susceptible to overexploitation due to targeted collection, non-selective fishing gear and habitat loss. Our findings indicate that overall densities of the species are low (0.0008 ± 0.0001 individuals/m^{-2}) and did not differ significantly between survey sites. Its abundance appeared to be relatively stable with no significant temporal changes noted during the study period. As our study sites comprised a variety of environmental characteristics ranging from bare sand substrate to seagrass meadows, this suggests *H. kuda* is a highly adaptive habitat generalist capable of utilizing its surroundings or migrating to more preferable areas. This highlights the potential resilience of the population compared to species with more specific requirements. Research on how population densities fluctuate seasonally is required to determine recruitment trends and additional variables such as water quality and holdfast choice must be studied to further understand the habitat preferences of *H. kuda* within the Koh Sdach Archipelago.

Keywords habitat generalist, *Hippocampus kuda*, non-invasive sampling, underwater visual census.

Introduction

Cambodia's coastal ecosystems underpin food security and offer valuable resources which increasingly play important roles in the Kingdom's socio-economic development, facilitating advances in infrastructure and attracting international tourists (RGC, 2016). Despite their importance, the paucity of peer-reviewed marine research in the country is stark, with only a few studies primarily focussing upon the biophysical characteristics of coral reef health to date (Chou *et al*., 2003; Savage *et al*., 2014; Thorne *et al*., 2015). For cryptic syngnathids, there are no published data related to their demographic characteristics, which hinders understanding of their population trends and limits conservation effort. This knowledge gap could be critical given the low biomass of fish in many areas of Cambodia, this being indicative of overexploited ecosystems, with the factors responsible for such declines posing an equal threat to seahorse populations (Glue *et al*., 2020).

Seahorses (*Hippocampus* spp.) belonging to the Syngnathidae are iconic marine fishes with significant ecological, economical and medicinal values (Vincent *et al*., 2011). Their emblematic morphology has resulted in their adoption as flagship species for conservation of marine and estuarine areas and they are important predators of bottom-dwelling species (Bologna, 2007; Vincent *et al*., 2011; Correia *et al*., 2018). However, seahorses are threatened by a myriad of factors including incidental capture in fisheries, exploitation for use in traditional medicines, collection for sale as curios and ornamental displays and degradation of essential habitats (Vincent *et al*., 2011). Their vulnerability is primarily due to life-history traits such as low mobility, small home ranges and mate fidelity, coupled with their tendency to inhabit shallow areas where anthropogenic disturbances are often recurrent (Lourie *et al*., 1999; Vincent *et al*., 2011; Gristina *et al*., 2015). These factors render seahorses particularly susceptible to population declines and have led to inclusion of the entire *Hippocampus* genus in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora. Several species are also classified as globally threatened on the International Union for Conservation of Nature (IUCN) Red List (Pollom *et al*., 2021).

Overexploitation, primarily by non-selective fisheries, has been identified as the leading threat to syngnathids, followed by habitat loss (Pollom *et al*., 2021). However, these threats are rarely isolated from the cumulative factors driving population declines. Anthropogenic influences are increasing at unprecedented rates and rapidly changing coastal areas around the world with the combined effects of development, destructive fishing techniques and unsustainable tourism causing severe habitat degradation (Crain *et al*., 2009). Associated factors including excessive boat traffic, nutrient enrichment, deterioration of water quality, and increased sedimentation, which typify Cambodian waters, evidently threaten marine communities and may well be leading to population patchiness (Browne *et al*., 2012; Correia, 2015; Claassens & Hodgson, 2018). The fact that habitat alterations have negative effects on seahorse species is well documented (Vincent, 1996). For instance, significant declines in populations of long-snouted seahorse *H. guttulatus* have occurred in seagrass meadows damaged by seining (Curtis *et al*., 2007) and the abundance of dwarf seahorse *H. zosterae* has been reduced by marina construction adjacent to seagrass habitats (Mason-Jones *et al*., 2010). As such, understanding the population parameters of species threatened with extinction is paramount to their conservation and this in turn is intrinsically linked to protection of their preferred habitats (Brown 1984; Harasti *et al*., 2014).

Determining the causes of population fluctuations is crucial for effective natural resource management (Kareiva, 1987; Clark, 2010; Correia, 2021). To achieve progress, conservation programmes require demographic data encompassing extant geographic distribution, habitat use, taxon-specific life-history characteristics and the relative influence of environmental disturbances in shaping populations (Thrush & Dayton, 2002; De Raedemaecker *et al*., 2010; Correia, 2015; Shapawi *et al*., 2015; Woodall *et al*., 2015). This information is typically utilized in three ways: in the design and implementation of habitat management areas; in communicating the scope and severity of threats; and in monitoring changes in the status of protected species. The latter is especially necessary for measuring success in halting biodiversity loss and the effectiveness of management areas (Bailie *et al*., 2004). It is imperative that conservation efforts focus on protecting hotspots that promote species density, particularly in areas where anthropogenic threats may have masked the magnitude of loss (Jackson *et al*., 2001; Pandolfi *et al*., 2003; Correia, 2015).

Progress is being made towards large-scale protection of ocean habitats in Cambodia with the proclamation of two marine protected areas (MPAs) since 2016. The Koh Sdach Archipelago (KSA) is the third location designated for development of a Marine Fisheries Management Area (MFMA) (FFI, 2020)—a national term for a type of multiple-use MPA. Within the archipelago, Koh Sdach village has opted to actively contribute to management of their marine resources through Cambodia's community fisheries (CFi) system. In many areas of the country, CFis are employed as legally recognised community-based organisations which are central in the design and management of MPAs (Roig-Boixeda *et al*., 2018). As a consequence, it is essential to understand the status of threatened marine species within the KSA to guide zonation processes and develop strategies that will maintain ecosystem functionality and promote the recovery of fisheries sustaining the local economy.

Five species of seahorse have been documented in Cambodia to date, namely *H. spinosissimus*, *H. kuda*, *H. mohnikei*, *H. trimaculatus* and *H. comes* (MCC, 2022). Among these, *H. kuda* is reportedly the most common in the Kingdom (Kuda Divers, 2021). With pressures mounting on the Cambodian marine environment (NESAP, 2016), we undertook a baseline assessment of the population dynamics of *H. kuda* within the KSA to assist its long-term conservation. Our study focussed on the distribution, abundance and population parameters of the species in five locations across the KSA, including data on sex, torso lengths and holdfast preferences. It was also based on non-invasive sampling techniques and designed to provide insights into population dynamics which can lead to more accurate estimations of responses to disturbance, survival and migration.

Methods

Study species

Hippocampus kuda is widely distributed throughout the Indo-Pacific region and is abundant in the Gulf of Thailand (Panithanarak *et al*., 2010), although it is currently classified as Vulnerable (Aylesworth, 2014) (Fig. 1). The species is thought to be a habitat generalist having been recorded in several inshore environments including mangroves, seagrass beds and estuaries (Lourie *et al*., 1999; Kuang & Chark, 2004; Ambo-Rappe *et al*., 2021) and is one of the most heavily-traded seahorse species in many Southeast Asian countries (Job *et al*., 2002).

Fig. 1 *Hippocampus kuda*, Koh Sdach Archipelago (© Roger Bruget).

However, few studies have investigated the population dynamics of *H. kuda* in-situ to our knowledge, although laboratory research has employed the species as a model organism (Choo & Liew, 2003; Kuang & Chark, 2004; Ambo-Rappe *et al*., 2021).

Study sites

The KSA comprises a collection of rocky islands in the Kiri Sakor District of Koh Kong Province, approximately 60 km southeast of Cambodia's border with Thailand (10°55′N, 103°5′E) (Fig. 2). The islands are predominantly uninhabited with the exception of Koh Sdach, which according to government census, is the most populated island on the Cambodian coast. Approximately 4,000 people inhabit Koh Sdach, over half of which are economically dependent on the fishing industry (FFI, 2020).

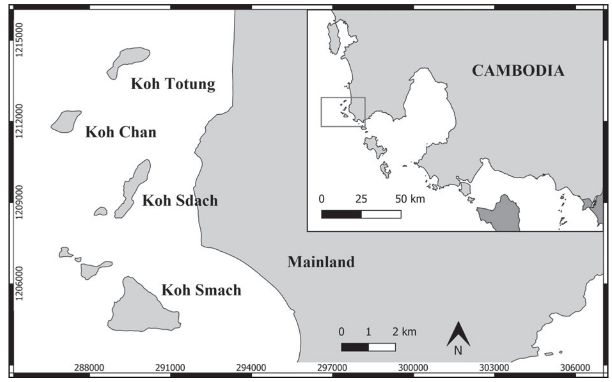

Fig. 2 Survey site locations in the Koh Sdach Archipelago, Cambodia (Mainland, Koh Totung, Koh Chan, Koh Sdach, Koh Smach).

Our research was conducted at five sites in the KSA which were surveyed by citizen science organizations at irregular intervals between December 2014 and April 2021. The five sites were selected based upon their differing environmental characteristics and were representative of potential seahorse habitat (Table 1).

Underwater visual census

We surveyed *H. kuda* using underwater visual census techniques based on the iSeahorse methodology (iSeahorse, 2014). The starting position and compass direction of each transect survey were randomly selected at the site and a GPS was used to obtain UTM coordinates for the start and end point of transects. Search times lasted approximately 60 minutes but varied depending on water conditions, as did the area searched. Search areas were calculated ex-situ and utilized the start and end coordinates to obtain their lengths in metres. As each surveyor searched the square metre directly in front of them, the search area was multiplied by the number of participants to determine total survey area.

For each seahorse sighted, photographs were taken with a ruler placed as close as possible to allow later measurement of biometric data. The species, sex and torso length of each individual were subsequently recorded on land (iSeahorse, 2014). Species were identified using information provided by Kuiter (2009) and for *H. kuda* included its characteristically long crown

Table 1 Details of sampling locations for underwater visual censuses of *Hippocampus kuda* in the Koh Sdach Archipelago, arranged from North to South.

Site	Substrate	Depth (m)	Habitat characteristics
Mainland	Sand & Silt	2.4–3.4	Bare sand substratum with seasonal sparse seagrass (*Halophila ovalis*); high boat traffic, high presence of discarded fishing gear (ropes, monofilament trammel nets), abandoned mooring piers.
Koh Totung	Sand	3.9–5.7	Predominantly seagrass meadow (*H. ovalis*, *Halodule uninervis* & *Cymodocea serrulata*) with seasonal fluctuations in density; Macroalgal mats (largely *Dictyota* sp.) dominate in May-June; little anthropogenic debris or disturbance.
Koh Chan	Sand	5.6–9.0	Sandy bottom; strong currents; trawler zone; anchor hotspot as a refuge boats during unfavourable weather.
Koh Sdach	Sand	4.7–6.9	Sandy bottom; high boat traffic and watersport activities, active gill and trammel nets present during surveys, some anthropogenic debris; the only site with a large settlement and no solid waste or sewage management systems operating on the island
Koh Smach	Sand & Silt	4.0–5.7	Seasonal sparse seagrass (*H. ovalis*); development on the island began in 2018 leading to high turbidity and silt substratum predominating in 2021

filaments, square head profile over the eye and smooth form. Seahorses with a full brood pouch were considered pregnant males and noted as such. Following Lourie *et al*. (1999), sex was assigned based on the presence (male) or absence (female) of a brood pouch. Environmental variables were also recorded, including the depth of occurrence, water temperature and holdfast at first sighting. Alongside data collected on transect surveys, 38 individuals were identified through roving sightings and although these were excluded from density calculations, their sex, torso length, and holdfast information were included in our dataset for analysis.

Statistical analyses

Descriptive statistics are reported as means ± standard error, unless stated otherwise. Comparative analyses of population density between sites and time periods were performed using generalized linear models (GLMs) which assumed a normal distribution with a log function. The data were transformed to normalize the distribution prior to model selection and summarised in Pearson chi-squared matrices to identify collinear variables as well as variables correlated with seahorse densities. Multiple regressions were carried out for seahorse densities between sampling sites and seasons (wet [May–October] vs. dry [November–April]) and the data were separated into two survey periods (2014–2017 and 2018–2021) to determine temporal fluctuations before and after major land use changes occurred in the study region. Successive GLMs to test torso length, holdfast and site were compared with previous models using either the 'ANOVA' or '*t*-test' function of the '*bioinfokit*' Python package followed by Tukey-Kramer tests to identify differences in the amount of variance.

Results

A total of 160 *H. kuda* were sighted over the course of 260 surveys completed during our study period. Three other seahorse taxa were also encountered during our surveys (*H. mohnikei*=33 individuals, *H. trimaculatus*=14, *H. spinosissimus*=6), but are not considered further in this study.

Hippocampus kuda had an overall density of 0.0008 (± 0.0001) individuals/m^{-2} across our study area. Densities per site ranged from 0.0002 (± 0.00007) individuals/m^{-2} (Koh Chan) to 0.0015 (± 0.0004) individuals/m^{-2} (mainland site) (Table 2), although there were no significant differences in mean density between locations (f=1.58, df=99, p=0.18). Sightings were greater during the dry season (0.0009 ± 0.0002 individuals/m^{-2}) compared to the wet season (0.0005 ± 0.0002 individuals/m^{-2}), although there were no significant differences between seasons (f=0.29, df=99, p=0.59) or specific months (f=1.41, df=249, p=0.17) (Fig. 3A). The more recent surveys in the KSA (2018–2021) revealed greater seahorse densities (0.00083 ± 0.00017 individuals/m^{-2}) compared to the 2014–2017 surveys (0.0007 ± 0.0001 individuals/m^{-2}). This was due to an increase at the mainland site, but no *H. kuda* were sighted at Koh Chan and minor declines occurred at all other sites in 2018–2021 (Fig. 4). However, the differences between the two periods and survey sites were not significant (f=0.04; df=99; p=0.84).

Overall, torso lengths of male *H. kuda* (49.00 ± 2.36 mm) were significantly larger than female (28.50 ± 1.21 mm) (t=7.58, df=47, p=1.084x10^{-9}) (Fig. 5), although they did not differ significantly between sites (f=0.86; df=192; p=0.49). The torso lengths of most individuals were between 13.97 mm and 47.69 mm, with a minimum of 8 mm and a maximum of 86 mm.

Table 2 Survey area, number of individuals and densities of *Hippocampus kuda* recorded at sampling sites within the Koh Sdach Archipelago.

Site	Surface area (m^2)	Number of individuals recorded	Mean density (individuals/m^{-2})	Mean density (individuals/km^{-2})
Mainland	43,037	41	0.0015 ± 0.0004	1.4538 ± 0.40318
Koh Totung	86,496	57	0.0009 ± 0.00016	0.9255 ± 0.16146
Koh Chan	60,941	14	0.0002 ± 0.00007	0.2854 ± 0.07010
Koh Sdach	75,924	34	0.0007 ± 0.00017	0.6535 ± 0.16701
Koh Smach	33,692	14	0.0006 ± 0.00023	0.6266 ± 0.22825
Koh Sdach Archipelago	30,090	160	0.0008 ± 0.0001	1.1080 ± 0.0937

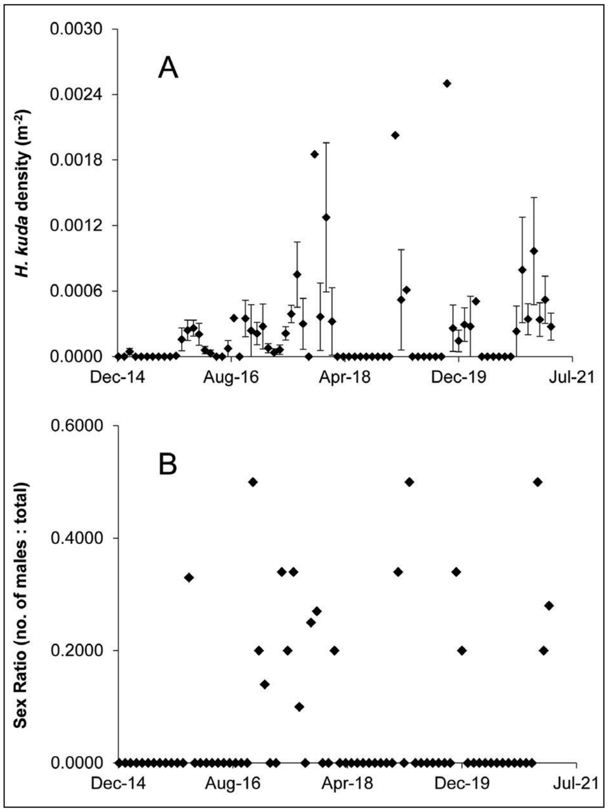

Fig. 3 Monthly densities (A) and sex ratios (B) of *Hippocampus kuda* within the Koh Sdach Archipelago from December 2014 to April 2021. Density data are given as mean (symbols) ± standard errors (bars).

Eighty-one percent of individuals whose sex was confirmed during the survey (*n*=163) were female, giving a male:female ratio of 1:4.26 (Fig. 3B). The dataset for sexes was insufficient for reliable comparisons between sites. Only 15 of seahorses recorded appeared to be pregnant males with swollen brood pouches and there was no noticeable seasonal pattern in their occurrence. The mean torso length of pregnant males was 51.92 ± 3.30 mm.

A large proportion of seahorses were not grasping any holdfast when recorded (36.55%). For individuals that were, 36.55% were associated with plant materials, 14.21% with fishing gear and 4.06% with invertebrates. The relative proportions of items employed as holdfasts varied between survey locations (Fig. 6) and reflected the abundance of site-specific benthic substrata. Macroalgae were the most commonly used holdfast at Koh Sdach (18.18%), whereas fishing gears (43.48%) were most frequently used at the mainland site, and seagrass (32.94%) was preferred at Koh Totung.

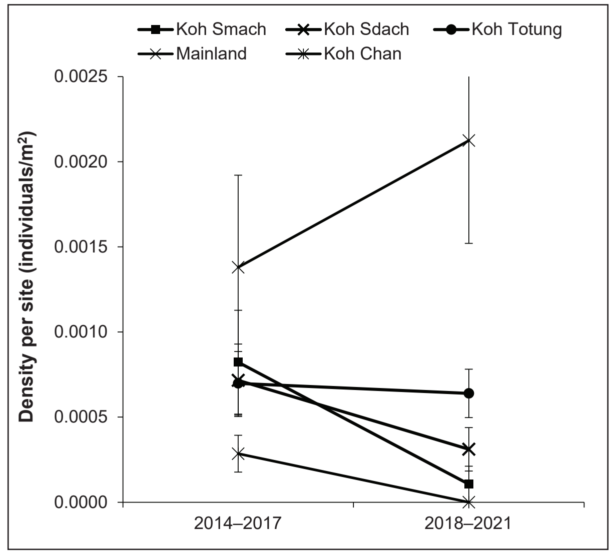

Fig. 4 Density of *Hippocampus kuda* recorded during two survey periods at five sites within the Koh Sdach Archipelago. Symbols represent means and bars represent standard errors.

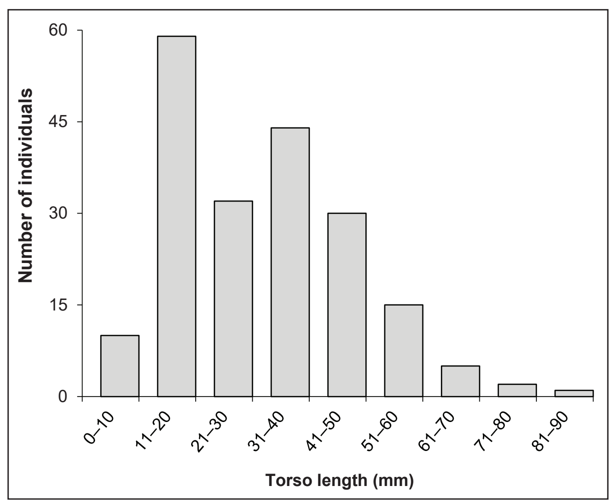

Fig. 5 Pooled frequency distribution of torso lengths for *Hippocampus kuda* within the Koh Sdach Archipelago (*n*=198).

Discussion

Ours is the first study to provide population parameters for the Vulnerable *H. kuda* seahorse in Cambodian waters. Population densities in the KSA are low at 0.0008 ± 0.0001 individuals/m^{-2} compared to similar generalists including *H. reidi* in Brazil (with 0.026 individuals/m^{-2}: Rosa *et al*. 2007), *H. zosterae* in Florida, USA (0.080 individuals/m^{-2}: Mason-Jones *et al*. 2010) and *H. hippocampus* in the Ria

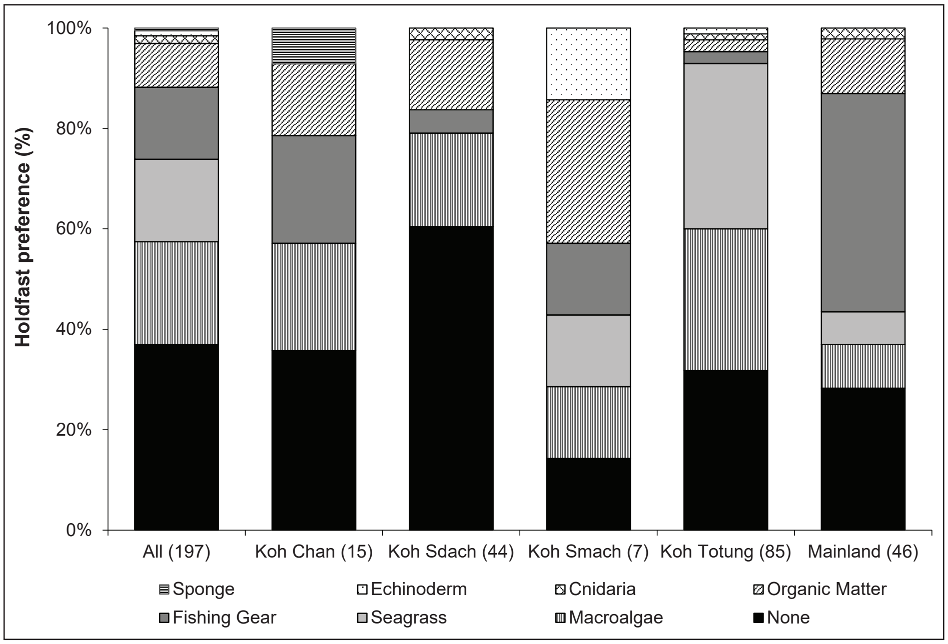

Fig. 6 Proportion of holdfasts utilized by *Hippocampus kuda* in sample sites and Koh Sdach Archipelago as a whole. Sample sizes are given in parentheses.

Formosa Lagoon of Portugal (0.008 individuals/m^{-2}: Correia, 2015). The limited availability of historical data for *H. kuda* in Cambodia and elsewhere in the world precludes comparisons of its abundance across its range. Our five survey locations were representative of a range of habitat characteristics and environmental variables within the KSA. As these sites were thought to be representative of seahorse habitats, our results provide insights into the drivers of seahorse paucity in the archipelago.

Our results suggest that the distribution of *H. kuda* in the KSA is not determined by habitat type and that the species occurs in a variety of dissimilar environments. Considering its distribution by site, *H. kuda* appears to be a habitat-generalist which occupies bare and complex environments in similar densities. This was contrary to our initial expectations as Kuang & Chark (2004) found that *H. kuda* preferred vegetation substrates in Malaysia, where individuals were consistently associated with *Enhalus acroroides* or *Halimeda* beds. In our study, the highest densities of *H. kuda* were recorded at the mainland site, where the predominant benthos comprises sand, with sparse, short *Halodule ovalis* only present for a portion of the year. It has been suggested that individuals encountered in habitats with bare substrates may be temporarily exploiting open habitats while transiting between preferred complex microhabitats or that these may have been displaced from their home ranges by currents (Curtis & Vincent, 2005). Additionally, the high energy conditions that occur during the southwest monsoon are likely to displace some seahorses from their territories but may also facilitate the recruitment of others (Choo & Liew, 2003). In our case, sightings of *H. kuda* repeatedly occurred across a gradient of seagrass meadows, macroalgal mats and near-shore open areas. This supports the notion that populations of the species in the KSA are capable of adapting to dynamic environments and are either exploiting their surrounding habitats or transiting between habitats. In general, species with broader habitat requirements are likely to show more resilience to disturbance compared to those with more specialized needs (Foster & Vincent, 2004).

Water quality and physical disturbance have been identified as possible factors in seahorse population declines (Martin-Smith & Vincent, 2005) and oceanographic and climatic conditions are known to influence *H. kuda* densities in Malaysia (Choo & Liew, 2003). The heavy rains that occur in Cambodia during the wet season from May to October are responsible for changes to its coastal ecosystems, with turbulent and low visibility waters typifying the KSA. During this period, siltation and runoff are high, with excess dissolved nutrients likely leading to reduced water quality (Krishna *et al*., 2016). In addition, coastal developments began in mainland areas adjacent to the archipelago in 2008 and infrastructure development accelerated on its islands in

2018, providing significant potential for transforming the marine environment (Nguyen, 2019). Some syngnathids respond poorly to associated pollutants and eutrophication which can manifest as disease (Koldewey & Martin-Smith, 2010) and while all of the individuals we observed appeared to be healthy, their vulnerability to stress cannot be ruled out despite their ability to tolerate poor quality environments. Reduced water visibility is also noteworthy as this has long been recognized as detrimental for seahorses. Since visual acuity is vital for feeding, reduced visibility can significantly reduce prey capture rates which may have broad implications for the reproductive success and survival of seahorses (James & Heck, 1994; Vincent *et al*., 2011; Correia *et al*., 2015a). While the waters of the archipelago are calm during the dry season (November to April), boat traffic increases markedly during this period, particularly at our mainland site and Koh Sdach. Boat noise has been defined as contributing to decreased populations of *H. capensis* (Claassens & Hodgson, 2018) and *H. erectus* has been shown to exhibit a physiological stress response to loud noise which leads to reduced body mass (Anderson *et al*., 2011). Indeed, distress has the potential to result in local extirpation of seahorse populations if poor conditions are continuous (Correia, 2021). However, some evidence also suggests that *H. zosterae* actively migrate from adverse shallow habitats towards deeper waters in search of more suitable surroundings (Mason-Jones *et al*., 2010). As the density of *H. kuda* did not appear to fluctuate significantly between seasons or over the wider study period, despite development activities in the KSA, this demonstrates the plasticity of the species and raises the possibility that individuals may be able to relocate from habitats they cannot endure to some extent.

Seahorses often display high site fidelity with small home ranges and low mobility (Kvarnemo *et al*., 2000; Foster & Vincent, 2004). However, their low density in the KSA and the temporal gaps between sightings of seahorses in successive surveys at the same locations suggests that its populations are likely mobile. Should individuals be dispersing however, this could potentially lead to their isolation, risking further declines in abundance due to fragmentation and reduced reproductive success of local populations (Correia *et al*., 2018). A myriad of anthropogenic stressors occur in the KSA and given the recently documented preference of *H. kuda* towards greater habitat complexity (Ambo-Rappe *et al*., 2021), these render it likely that populations of the species can tolerate fluctuations in environmental conditions. As such and similar to other *Hippocampus* spp. in Portugal (Correia *et al*., 2018), *H. kuda* could be occupying alternate, less preferable areas within the KSA which ultimately become their selected habitats.

We found that holdfast choice in the KSA clearly reflected the available benthos at our survey sites. Individuals encountered at the mainland site primarily employed fishing gear (e.g., discarded nets, rope, line) as a holdfast, which might be due to the diminished availability of natural structures mandating that they become holdfast generalists. This preference may also be a consequence of the artificial structures hosting fewer predators and competitors than seagrass meadows, in addition to being food rich (Morgan & Vincent, 2007; Correia, 2015). At the majority of our sites, the individuals we observed did not utilize any holdfast at all, even when in the presence of expected choices. This could be attributable to these habitats serving as temporary settlements while H. kuda move towards preferred environments. Given their limited mobility, seahorses are reliant on holdfasts for anchoring, particularly in areas that may be strongly influenced by hydro-dynamics (Harasti *et al*., 2014; Aylesworth *et al*., 2015). In the Ria Formosa lagoon of Portugal, a highly dynamic area where strong currents characterize the environment, stable holdfasts are vital in ensuring seahorse populations are not swept away from their preferred habitats and *H. guttulatus* has been found to grasp close to the base of structures to minimize instability (Correia *et al*., 2015b). At all of our survey sites, a number of individuals were observed clinging to drift macroalgae. Algal biomass is a key refugia utilized by juvenile and subadult *H. hippocampus* in Gran Canaria (Otero-ferrer, 2015) and as we encountered *H. kuda* adults attached to these fronds, it could be that the algae provides a viable method of dispersal rather than security. If found to the case, this possibility would be consistent with reports for *Syngnathus fuscus* and *H. zosterae* in the USA (Able *et al*., 2002; Mason-Jones *et al*., 2010) and further establish *H. kuda* as a mobile species.

Artificial structures have been employed to combat the degradation of natural ecosystems by creating alternative habitats. This has been successful in aiding several *Hippocampus* species by providing opportunities for predator avoidance, hunting and reproduction (Hellyer *et al*., 2011; Correia *et al*., 2015b; Otero-Ferrer *et al*., 2015; Simpson *et al*., 2020). As anthropogenic debris is utilized by *H. kuda* at multiple sites in the KSA, artificial structures could potentially be beneficial in preferred habitats within the region that have been degraded and lack holdfasts. Strap-like leaf forms of seagrass have been found to be important for *H. kuda* in other studies (Kuang & Chark, 2004; Ambo-Rappe *et al*., 2021) and further research into holdfast choices in the KSA will aid in determining if preferences exist within its populations of the species.

We found male *H. kuda* had significantly longer torso lengths than females across all sites. Total height has also been found to be significantly longer in male *H. capensis*, with longer tails and shorter heads observed (Bell *et al*., 2003; Claassens & Hodgson, 2018). Longer tails are common to Syngnathidae and believed to allow individuals with larger caudal pouches to either securely grasp holdfasts or assist tail-wrestling (Vincent, 1990). It is uncommon for size between sexes to significantly differ (Otero-Ferrer *et al*., 2015). Although reproductive success is not always linked to size of an individual, larger individuals have been shown to yield increased young (Vincent & Giles, 2003; Rosenqvist & Berglund, 2011). Kvarnemo *et al*. (2007) established that sexual selection can be substantial and act on males in certain species that can be both monogamous and polygynandrous. As such, larger males may be an adaptive approach utilized in mobile, low-density populations (which are probable in the KSA) where meetings are infrequent and time for assessing potential mates is limited.

Adult sex ratios vary greatly among *Hippocampus* spp. with female-biased sex ratios, such as in the present study, typical of *H. abdominalis* in Australia (Martin-Smith & Vincent, 2005), *H. hippocampus* in the Macaronesian Islands (Otero-Ferrer *et al*., 2015) and *H. erectus* in the USA (Teixeira & Musick, 2001). A pair of seahorses were not sighted at any point during our surveys and this could suggest a lack of mate fidelity and evidence of polygynandry within the population. One possible explanation for the excess of females is an increased mortality rate for the opposite sex—since males are larger they are more visible and therefore more frequently predated upon (Claassens & Hodgson, 2018). Populations with heavily-skewed sex ratios have shown reduced reproductive success (Kvarnemo *et al*., 2007) and understanding the preferences of *H. kuda* in the KSA could be of high importance to the future of populations there.

It is important to outline the key limitations of our study. The scope of our work was restricted by the capacity of researchers in the citizen science organisations who assisted our fieldwork, with temporal gaps also existing in the data. This meant our analyses of seasonality were limited by decreased activity during the monsoon season and further understanding of reproductive activity and recruitment was not possible. Our sampling was biased towards Koh Totung and the mainland site which were surveyed orders of magnitudes more than others due to factors including reduced swell and better visibility. As such, the condensed survey effort in some areas may have contributed towards the low abundance recorded or even the notable absences at certain sites. While these constraints reduced the likelihood of identifying significant trends or population predictability, there was still sufficient data to complete our purposes of providing a baseline of data that can be employed for localised, site-specific protection of *H. kuda*.

Successful protection and management of threatened species are only possible with up to date information on populations and life history traits. Ours is the first study to describe the ecology of *H. kuda* in the coastal environment of Cambodia. Our findings indicate that population densities are low but further research on environmental variables is required to define the specific factors responsible for seahorse demographics. Ecological monitoring plays a vital role in determining when a system has been altered from a desired state as well as informing the success of conservation actions (Legg & Nagy, 2006; Claassens & Harasti, 2020). As such, our research provides a reference point regarding the status of *H. kuda* within the KSA and continued research will confirm the effectiveness of zonations proposed for the MFMA. Our observations also highlight the potential mobility of *H. kuda* and provide evidence the species may be a habitat and holdfast generalist capable of adapting to changing environments. This plasticity may well have ensured the survival of local populations despite ongoing threats in the KSA. Ongoing research will be vital to confirm population densities and determine if monthly fluctuations occur in these. This information will aid in determining recruitment trends and amplify existing knowledge which can support measures that provide a foundation for biodiversity recovery (Glue *et al*., 2020).

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About the authors

Jess Kalisiak worked in the Koh Sdach Archipelago for much of 2021 redefining methods employed in conservation projects undertaken by Kuda Divers. These included studies of the growth rates of marine sponge *Cliona patera*, population dynamics of seahorses, coral reef health and seagrass abundance, all of which provided data to support the management of marine protected areas.

Ian Gray has lived on the coast of Cambodia for three years and is a marine enthusiast, diver and keen coder and statistician who primarily works with the Python programming language.

Roger Bruget is the founder and owner of Kuda Divers. Having worked in the Koh Sdach Archipelago for almost a decade, he has extensive knowledge on changes in the marine environment of the archipelgao over time.

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Recent Master's Theses

This section presents the abstracts of research theses produced by Royal University of Phnom Penh graduates recently awarded the degree of Masters of Science in Biodiversity Conservation. The abstracts have been edited for English and brevity.

Assessment of macroinvertebrate communities, water quality and ecosystem provisioning services in Kbal Chhay Multiple Use Area, Preah Sihanouk Province

CHHORN Soksan

មូលន័យសង្ខេប

សត្វឥតឆ្អឹងកងត្រូវបានគេប្រើប្រាស់យ៉ាងទូលំទូលាយធ្វើជាសូចនាករជីវសាស្ត្រក្នុងប្រព័ន្ធអេកូឡូស៊ីទឹកសាប ប៉ុន្តែសហាគមន៍របស់សត្វឥតឆ្អឹងកងជាមួយនិងសន្ទស្សន៍គុណភាពទឹកផ្សេងៗត្រូវបានគេសិក្សាតិចតួចណាស់នៅប្រទេសកម្ពុជា។ គោលបំណងនៃការសិក្សានេះ គឺដើម្បីអង្កេតមើលពីទំនាក់ទំនងរវាងសហាគមន៍សត្វឥតឆ្អឹងកងជាមួយនឹងប៉ារ៉ាម៉ែត្រគុណភាពទឹកនៅតំបន់ប្រើប្រាស់ច្រើនយ៉ាងព្រែកទឹកសាបក្បាលឆាយ និងធ្វើការព្យាករណ៍អំពីសេវាផ្គត់ផ្គង់ទឹកនៅតំបន់នេះ។ សំណាញ់ដៃ និងការធ្វើតេស្តប៉ារ៉ាម៉ែត្របរិស្ថានផ្សេងៗត្រូវបានប្រើដើម្បីប្រមូលសំណាកសត្វឥតឆ្អឹងកង និងទិន្នន័យគុណភាពទឹកពីទីតាំងចំនួន២៦ នៅតំបន់សិក្សានេះ ក្នុងខែតុលា ឆ្នាំ២០២០។ សត្វឥតឆ្អឹងកងសរុបចំនួន៥៨២ក្បាល ដែលស្ថិតក្រោម៤១ចំណាត់ថ្នាក់ ៣០អំបូរ ១៣លំដាប់ និង៤ថ្នាក់ ត្រូវបានកត់ត្រា។ ថ្នាក់ដែលមានចំនួនលើសលុបបំផុតគឺថ្នាក់ Insecta (ប្រហែល៨០%នៃទីតាំងដែលបានប្រមូល) បន្ទាប់មកគឺថ្នាក់ Malacostraca (១០%) ហើយថ្នាក់Gastropoda (១០%) និងថ្នាក់Pelecypoda (០.២%)។ សត្វឥតឆ្អឹងកងនៅក្នុងការសិក្សានេះត្រូវបានចែកជា០២ក្រុមធំៗដោយ cluster analyses នៃរចនាសម្ព័ន្ធសហាគមន៍ ភាពសម្បូរបែប និងនានាភាពនៃប្រភេទដែលមានការកើនឡើងពីព្រែកផ្នែកខាងលើ(ក្រុមទី១) ទៅទីតាំងព្រែកផ្នែកខាងក្រោម(ក្រុមទី២)។ ប្រភេទជាសូចនាករនៅក្នុងក្រុមទី១ រួមមាន insects (ដូចជា *Hydrometra sp.* និង *Mesovelia sp.*) និងក្រុម molluscs (ដូចជា *Pila gracilis*) ខណៈនៅក្នុងក្រុមទី២ គឺមានតែក្រុម insects តែប៉ុណ្ណោះ (ដូចជា *Rheumatogonus sp.* និង *Hydropsychinae sp.*)។ សហាគមន៍សត្វឥតឆ្អឹងកងក្នុងក្រុមទី១ មានទំនាក់ទំនងជាមួយនឹងសីតុណ្ហភាពខ្ពស់ រយៈទទឹងខ្ពស់ និងចរន្តកម្រិតរំលាយសារធាតុរឹងសរុបខ្ពស់ ចំណែកឯសហាគមន៍សត្វឥតឆ្អឹងកងក្នុងក្រុមទី២ មានទំនាក់ទំនងជាមួយនឹងកម្រិតទឹកភ្លៀងខ្ពស់ ភាគរយគម្របព្រៃឈើច្រើន ទំហំថ្មមធ្យមច្រើន និងភាពធន់ខ្ពស់។ កម្រិតបំពុលខ្ពស់ត្រូវបានរកឃើញនៅទីតាំងក្រុមទី១ ដែលជម្រកទឹកនៅទីតាំងនេះភាគច្រើនគ្របដណ្តប់ទៅដោយទឹកនឹង និងព័ទ្ធជុំវិញដោយតំបន់សាងសង់ ទេសចរណ៍ និងតំបន់ដីកសិកម្ម។ ទឹកត្រូវបានកំណត់ថាជាសេវាកម្មផ្គត់ផ្គង់ដ៏សំខាន់នៅក្នុងតំបន់ប្រើប្រាស់ច្រើនយ៉ាងព្រែកទឹកសាបក្បាលឆាយ ហើយផ្អែកលើនិន្នាការបច្ចុប្បន្ន ការប្រើប្រាស់ទឹកនៅតំបន់នេះនឹងឈានហួសសមត្ថភាពដែលអាចផ្គត់ផ្គង់បាននៅចុងឆ្នាំ ២០២៣។ ជារួម លទ្ធផលនៃការសិក្សារបស់ខ្ញុំបង្ហាញថា ការសឹករិចរិលនៃទីជម្រក និងការរំខានដោយសកម្មភាពមនុស្សបានបង្កឱ្យ មានការថយចុះនូវភាពសម្បូរនៃប្រភេទ និងចំនួនឯកត្តៈនៃសហាគមន៍សត្វឥតឆ្អឹងកងនៅទីតាំងជាក់លាក់មួយចំនួនក្នុងតំបន់ប្រើប្រាស់ច្រើនយ៉ាងព្រែកទឹកសាបក្បាលឆាយ។

Abstract

Although the utility of macroinvertebrates as bioindicators in freshwater ecosystems is well known, their assemblages and associated water quality indices are poorly documented in Cambodia. The aim of this study was to investigate relationships between macroinvertebrate assemblages and water quality parameters in the Kbal Chhay Multiple Use Area (KCMUA) and predict water provisioning services at the site. To this end, hand nets and multiple parameter tests were employed to sample macroinvertebrates and water quality at 26 locations within the protected area in October 2020. A total of 582 macroinvertebrates representing 41 taxa belonging to 30 families, 13 orders and four classes were recorded. The most dominant class was Insecta (ca. 80% of sites), followed by Malacostraca (10%), Gastropoda (10%) and finally Pelecypoda (0.2%). Two major groups were apparent in cluster analyses of assemblage structure and species richness

and diversity increased from upstream (Group I) to downstream (Group II) areas. Indicator species in Group I included insects (e.g., *Hydrometra* sp., *Mesovelia* sp.) and molluscs (e.g., *Pila gracilis*), whereas those in Group II solely comprised insects (e.g., *Rheumatogonus* sp., *Hydropsychinae* sp.). Group I assemblages were associated with higher temperatures, altitude, conductivity and total dissolved solids, whereas Group II assemblages were associated with higher rainfall, forest cover, medium-sized stone substrates and resistivity. High pollution levels were observed at Group I sites where aquatic habitats largely comprised standing waters surrounded by construction, tourism and agricultural areas. Water was identified as an important provisioning service in the KCMUA and based on current trends, consumption of water will reach the carrying capacity of the site by the end of 2023. Overall, my findings suggest that habitat degradation and anthropogenic disturbance have reduced the taxonomic richness and abundance of macroinvertebrate assemblages in certain areas of KCMUA.

Seasonal and geographical variations in the diet of lesser yellow house bat *Scotophilus kuhlii* Leach, 1821 populations in Cambodia

SIN Sopha

មូលន័យសង្ខេប

កសិកម្មដោយចីរភាពមានសារៈសំខាន់ខ្លាំងណាស់ដល់សន្តិសុខស្បៀងនៅកម្ពុជា។ ប្រចៀវស៊ីសត្វល្អិតជាអ្នកកម្ចាត់សត្វល្អិតដែលបំផ្លាញដំណាំកសិកម្មយ៉ាងមានប្រសិទ្ធភាព ដែលសេវាកម្មនេះកំពុងជួយសន្សំប្រាក់ដល់កសិករបានរាប់ពាន់លានដុល្លារក្នុងមួយឆ្នាំនៅទូទាំងពិភពលោក។ ទោះជាយ៉ាងនេះក្តី រហូតមកដល់ពេលនេះមានការសិក្សាតែមួយគត់ដែលបានកត់ត្រាអំពីសត្វប្រចៀវស៊ីសត្វល្អិតនៅក្នុងប្រទេសកម្ពុជា។ ការសិក្សានេះមានគោលបំណងវាយតម្លៃអំពីបម្រែបម្រួលរដូវកាល និងទីតាំងភូមិសាស្ត្រនៃរបបអាហាររបស់សត្វប្រចៀវ *Scotophilus kuhlii* ដែលជាប្រភេទស៊ីសត្វល្អិតនៅលើអាកាស មានរបាយធំ និងសំបូរនៅតាមតំបន់កសិកម្មនៃប្រទេសកម្ពុជា។ លាមករបស់ប្រចៀវនេះត្រូវបានប្រមូលនៅខេត្តកណ្តាល និងកំពង់ចាម (ភាគខាងត្បូង) និងខេត្តពោធិ៍សាត់ និងបន្ទាយមានជ័យ (ភាគខាងលិច) ក្នុងរដូវប្រាំង (មីនាដល់មេសា) និងរដូវវស្សា (មិថុនាដល់កក្កដា) ក្នុងឆ្នាំ២០២០។ សំណាកចំនួន២០ត្រូវបានវិភាគដោយប្រើប្រាស់មីក្រូទស្សន៍ទៅតាមខែ និងតាមទីតាំងនីមួយៗ។ ក្រៅពីពពួកចៃ និងពីងពាង មានសត្វល្អិត៨លំដាប់ត្រូវបានរកឃើញពីសំណាកដែលប្រមូលបានពីខេត្តកណ្តាល កំពង់ចាម និងពោធិសាត់ និងសត្វល្អិតចំនួន៩លំដាប់បានរកឃើញពីសំណាកប្រមូលបានពីខេត្តបន្ទាយមានជ័យ។ បើគិតពីភាគរយវិញ Coleoptera (Scarabaeidae និង Curculionidae) និង Heteroptera (Lygaeidae និង Pentatomidae) គឺជាលំដាប់ដែលត្រូវបានឃើញច្រើនជាងគេនៅរដូវប្រាំង ខណៈដែល Coleoptera និង Blattellidae រកឃើញច្រើននៅរដូវវស្សា (និងមានតិចតួចនៅក្នុងសំណាកពីខេត្តបន្ទាយមានជ័យ)។ ការប្រៀបធៀបដោយផ្អែកលើភាគរយមធ្យមនៃបរិមាណចំណីដែលវាបានស៊ី បានបង្ហាញពីភាពខុសគ្នាខ្លាំងនៅក្នុងសមាមាត្រពី៣ ទៅ៥ អំបូរសត្វល្អិតដែលស៊ីដោយប្រចៀវ *S. kuhlii* ក្នុងខេត្តនីមួយៗរវាងរដូវប្រាំង និងរដូវវស្សា។ ភាពខុសគ្នានេះអាចមកពីប្រចៀវប្រភេទនេះមានរបបអាហារទូទៅដែលអាចសម្របរបបអាហាររបស់វាទៅតាមចំណីដែលមានក្នុងទីតាំងនិងពេលវេលាជាក់លាក់មួយ។ ភាពបត់បែនបានទៅតាមរបបអាហារនេះ បង្ហាញថាប្រចៀវ *S. kuhlii* អាចដើរតួនាទីយ៉ាងសំខាន់ក្នុងការកម្ចាត់សត្វល្អិតចង្រៃពេញមួយឆ្នាំ ជាពិសេសប្រហែល៨៥%នៃអំបូរសត្វល្អិតដែលបានកំណត់អត្តសញ្ញាណក្នុងការសិក្សានេះ ជាអំបូរសត្វល្អិតចង្រៃសម្រាប់កសិកម្ម។ ជាលទ្ធផល វិធានការដូចជាការផ្តល់ជម្រក អាចជួយឱ្យប្រចៀវ *S. kuhlii* រស់នៅក្នុងតំបន់កសិកម្ម ក៏ដូចជាការកិច្ចខិតខំប្រឹងប្រែងសិក្សាស្រាវជ្រាវដើម្បីលើកម្ពស់ការយល់ដឹងឱ្យកាន់តែទូលំទូលាយអំពីសេវាកម្មគ្រប់គ្រងសត្វល្អិតដែលផ្តល់ដោយប្រចៀវប្រភេទនេះ និងប្រចៀវស៊ីសត្វល្អិតប្រភេទផ្សេងៗទៀតនៅក្នុងប្រទេសកម្ពុជា។

Abstract

Sustainable agriculture is crucial to food security in Cambodia. Insectivorous bats are effective suppressors of agricultural pests and this service saves farmers billions of dollars every year worldwide. Despite this, only one study

has documented the prey consumed by insectivorous bats in Cambodia to date. The aim of my study was to evaluate seasonal and geographical variation in the diet of the lesser yellow house bat *Scotophilus kuhlii*, a wide-ranging aerial insectivore common in agricultural landscapes throughout the country. Faecal samples were collected from the Kandal and Kampong Cham (southern) and Pursat and Banteay Meanchey (western) provinces during the dry (March–April) and wet (June–July) seasons in 2020. Twenty of these samples were analysed by microscopy for each month at each site. Alongside mites and spiders, eight insect orders were identified in samples from Kandal, Kampong Cham and Pursat and nine in samples from Banteay Meanchey. In terms of percentage frequency, Coleoptera (Scarabaeidae and Curculionidae) and Heteroptera (Lygaeidae and Pentatomidae) dominated samples during the dry season, whereas Coleoptera and Blattellidae dominated samples during the wet season (although less so in Banteay Meanchey). Comparisons based on the mean percentage volume of prey items revealed significant differences in the relative proportions of 3–5 insect families consumed by *S. kuhlii* in each province between the dry and wet seasons. These differences are likely due to the species being a dietary generalist which can opportunistically adjust its diet to the prey available at a given place and time. This flexibility suggests *S. kuhlii* could play an important role in suppressing pest outbreaks throughout the year, particularly as approximately 85% of the families identified during the study include economically-significant agricultural pests. As a result, measures such as roost provision that would benefit populations of *S. kuhlii* are warranted in agricultural landscapes, as are efforts to improve understanding and wider awareness of the pest control services provided by this and other insectivorous bat species in Cambodia.

Assessing the population status of striped catfish *Pangasianodon hypopthalmus* (Sauvage 1878) in the Cambodian Lower Mekong system

SOEM Sothearith

មូលន័យសង្ខេប

ត្រីប្រាធំ គឺជាប្រភេទត្រីដែលត្រូវបានជ្រើសរើសដើម្បីលើកកម្ពស់គាំទ្រការអភិរក្សជីវចម្រុះ (flagship species) នៅទន្លេមេគង្គ ដែលវាមានតម្លៃសំខាន់ខាងពាណិជ្ជកម្មក្នុងវិស័យជលផល និងពេញនិយមក្នុងវារីវប្បកម្មនៅក្នុងប្រទេសជាច្រើនក្នុងតំបន់ ទន្លេមេគង្គ។ ជាប្រភេទត្រីកំពុងស្ថិតក្នុងភាពរងគ្រោះ ស្ថានភាពប៉ូពុយឡាស្យុងរបស់ត្រីប្រាធំនៅក្នុងប្រព័ន្ធទន្លេមេគង្គប្រទេសកម្ពុជានៅមិនទាន់មានការយល់ច្បាស់នៅឡើយ។ ខ្ញុំបានប្រើកម្មវិធីម៉ូដែល (linear regression) ដើម្បីអង្កេតមើលអំពីបម្រែបម្រួលនៃទម្ងន់ផលចាប់របស់ត្រីប្រាធំពេញវ័យ ដែលទិន្នន័យត្រូវបានប្រមូលពីដាយចំនួន៦៤នៅទន្លេសាប ក្នុងអំឡុងពេលនៃរដូវនេសាទ ពីខែតុលា ដល់មីនា ឆ្នាំ១៩៩៨ ដល់ឆ្នាំ២០១៨។ បន្ទាប់មក ខ្ញុំបានធ្វើការវិភាគដោយប្រើប្រាស់ surveillance plot ក្នុងការ វាយតម្លៃពីរបាយទិន្នន័យនៃរង្វាស់ប្រវែងដែលត្រូវបានប្រមូលពីដាយនេសាទនៅទន្លេសាប ក្នុងអំឡុងរដូវនេសាទពីឆ្នាំ ២០០១ ដល់ ២០១៩។ ខ្ញុំក៏បានធ្វើការសិក្សាទៅលើបម្រែបម្រួលនៃចំនួនឯកត្តៈរបស់កូនត្រីប្រាធំតាមរយៈ linear regression ដែលទិន្នន័យ ត្រូវបានប្រមូលនៅរវាងខែមិថុនា ដល់ខែកញ្ញា ពីឆ្នាំ២០០៤ - ២០១៨ នៅទន្លេមេគង្គក្នុងរាជធានីភ្នំពេញ។ ជាចុងក្រោយ ខ្ញុំក៏បាន ធ្វើការអង្កេតទៅលើទំនាក់ទំនងរវាងទម្ងន់ផលចាប់នៃឯកត្តៈត្រីប្រាធំពេញវ័យនៅដាយនេសាទក្នុងទន្លេសាប ជាមួយនឹងសូចនាករ ទឹកជំនន់ និងទិន្នន័យចំនួនឯកត្តៈរបស់កូនត្រីប្រាធំពីឆ្នាំ២០០៥ - ២០១៧ ដោយប្រើ multiple linear regression ម៉ូដែល។ អត្រាខ្ពស់នៃការចាប់បានត្រីប្រាធំពេញវ័យ គឺមាននៅដើមរដូវនេសាទ (ពីខែតុលា ដល់ វិច្ឆិកា) ខណៈដែលអត្រាទាបនៃការចាប់បានត្រីប្រាធំពេញវ័យ គឺមាននៅក្នុងអំឡុងពេលពីខែ កុម្ភៈ ដល់ មីនា។ ទម្ងន់ផលចាប់នៃត្រីប្រាធំពេញវ័យនៅដាយនេសាទក្នុងទន្លេសាប មានការធ្លាក់ចុះចន្លោះពីឆ្នាំ១៩៩៨ ដល់ ឆ្នាំ២០១៨ ដែលនេះរួមបញ្ចូលទាំងសមាមាត្រនៃផលចាប់សរុបរបស់ប្រភេទត្រីផ្សេងទៀត ផងដែរ។ ទំហំឯកត្តៈរបស់ត្រីប្រាធំនៅទន្លេសាបក៏មានការថយចុះផងដែរនៅរវាងពីឆ្នាំ២០០៣ ដល់ ឆ្នាំ២០១៩ ហើយចំនួនឯកត្តៈនៃកូនត្រីប្រាធំនៅទន្លេមេគង្គក្នុងរាជធានីភ្នំពេញមានការថយចុះតិចតួចផងដែរនៅរវាងពីឆ្នាំ២០០៤ ដល់ ឆ្នាំ២០១៨។ ទម្ងន់ផលចាប់នៅ ដាយនេសាទមានទំនាក់ទំនងជាវិជ្ជមានជាមួយសូចនាករទឹកជំនន់ ហើយក៏មានទំនាក់ទំនងវិជ្ជមានជាមួយចំនួនកូនត្រីផងដែរ តែស្ថិតក្នុងកំរិតទាបជាងសូចនាករទឹកជំនន់។ លទ្ធផលនៃការសិក្សារបស់ខ្ញុំបង្ហាញថា ការគ្រប់គ្រងជលផលទៅថ្ងៃអនាគតគួរតែផ្តោតទៅលើការថែរក្សា

លំហូរទឹកនៅដងទន្លេសាប និងការរសាត់កូនត្រីប្រាធំពីទន្លេមេគង្គទៅកាន់តំបន់ទំនាបលិចទឹក ក្នុងគោលបំណងអភិរក្សប៉ូពុយឡាស្យុងត្រីប្រាធំនៅអាងទន្លេមេគង្គក្រោម។

Abstract

The striped catfish *Pangasianodon hypopthalmus* is a flagship species inhabiting the Mekong River, commercially important in fisheries and popular in aquaculture in many countries in the region. While Endangered, the status of its populations in the Cambodian Mekong system are not well understood. I employed linear regression to firstly investigate temporal variations in the catch weight of adult striped catfishes collected from 64 Dai units in the Tonle Sap River during the October–March fishing seasons from 1998 to 2018. I then conducted surveillance plot analysis to evaluate the distribution of length data collected in the Tonle Sap Dai fishery during the 2001 to 2019 fishing seasons. Following this, I explored temporal trends in the abundance of striped catfish larvae and juveniles through linear regression of data collected between June and September each year from 2004 to 2018 in the Mekong River in Phnom Penh. Finally, I investigated the relationships between the catch weight of adult individuals from the Tonle Sap Dai fishery and flood indices and larval abundance data from 2005 to 2017 using a multiple linear regression model. High proportions of adult striped catfish were caught at the start of the fishing season (October–November) whereas proportions were low later in the season (February–March). The catch weight of adult fish in Tonle Sap Dai fishery declined between 1998 and 2018, including as a proportion of the total catch of other species. The size of individuals in the Tonle Sap River also declined between 2003 and 2019 and a slight decline occurred in the abundance of larvae in the Mekong River in Phnom Penh between 2004 and 2018. Catch weights in the Dai fishery were positively associated with flood indices and to a lesser extent with larval abundance. My results suggest that future fisheries management should focus on maintaining water flows along the Tonle Sap River as well as fish larvae drift from the Mekong River to floodplain areas to conserve populations of striped catfish in the Lower Mekong Basin.

Distribution of two small mud carps across space and time in the Lower Mekong Basin

SUP Mecta

មូលន័យសង្ខេប

ត្រីរៀលអង្កាម និងត្រីរៀលគុប គឺជាប្រភេទត្រីសំខាន់បំផុតសម្រាប់ពាណិជ្ជកម្ម និងជាប្រភេទត្រីដែលសំខាន់ (keystone species) នៅតំបន់អាងទន្លេមេគង្គក្រោម។ តែយ៉ាងណាក្តី ព័ត៌មានអំពីរបាយទៅតាមទីតាំង និងពេលវេលារបស់ត្រីទាំងពីរប្រភេទនេះនៅក្នុងអាងទន្លេមេគង្គក្រោម គឺមានការសិក្សាតិចតួចនៅឡើយ។ ការសិក្សារបស់ខ្ញុំធ្វើឡើងដោយផ្អែកទៅលើទិន្នន័យដែលប្រមូលបានពីទីតាំងចំនួន២២ នៅតំបន់អាងទន្លេមេគង្គក្រោម ចាប់ពីឆ្នាំ ២០០៧ ដល់ឆ្នាំ២០១៥ ដោយមានគោលបំណង ១) វាយតម្លៃអំពីចំនួនឯកត្តៈ និងជីវម៉ាសនៃត្រីទាំងពីរប្រភេទនេះនៅក្នុងអាងទន្លេមេគង្គក្រោម ២) ស្វែងយល់អំពីភាពចម្រុះនៃចំនួនប៉ូពុយឡាស្យុងរបស់ត្រីទាំងពីរប្រភេទនេះទៅតាមពេលវេលា និង ៣) ធ្វើការអង្កេតទៅលើកត្តាផ្សេងៗដែលកំណត់លក្ខណៈទាំងនេះ។ ការសិក្សារបស់ខ្ញុំរកឃើញថា ត្រីរៀលអង្កាមមានចំនួនច្រើននៅក្នុងប្រទេសកម្ពុជា (បឹងទន្លេសាប ទន្លេសាប និងទន្លេមេគង្គ) ប៉ុន្តែវាមានចំនួនតិចនៅប្រទេសឡាវ និងដីសណ្តទន្លេមេគង្គ (វៀតណាម) ខណៈដែលត្រីរៀលគុបមានចំនួនច្រើននៅតំបន់ដីសណ្តទន្លេមេគង្គ និងបឹងទន្លេសាប ប៉ុន្តែវាមានចំនួនតិចនៅតំបន់ប្រព័ន្ធទន្លេ ស៣ (ប្រទេសកម្ពុជា) និងនៅប្រទេសឡាវ។ ប៉ូពុយឡាស្យុងរបស់ត្រីរៀលអង្កាមមានការធ្លាក់ចុះខ្លាំងនៅអំឡុងពេលនៃការសិក្សានៅបឹងទន្លេសាប ប្រព័ន្ធទន្លេ ស៣ និងទន្លេមេគង្គក្នុងប្រទេសកម្ពុជា ខណៈដែលប៉ូពុយឡាស្យុងរបស់ត្រីរៀលគុប មានការធ្លាក់ចុះនៅទីតាំងមួយចំនួននៅក្នុងប្រទេសវៀតណាម និងប្រទេសកម្ពុជា (បឹងទន្លេសាប)។ ប៉ូពុយឡាស្យុងរបស់ត្រីរៀលទាំងពីរប្រភេទនេះនៅទីតាំងដទៃផ្សេងទៀតមានលក្ខណៈថេរ។ លទ្ធផលរកឃើញពីការសិក្សារបស់ខ្ញុំបង្ហាញថាលក្ខណៈទាំងនេះត្រូវបានកំណត់ដោយកត្តាផ្សេងៗនៃបរិស្ថាន។ ឧទាហរណ៍ ចំនួនឯកត្តៈរបស់ប្រភេទត្រីរៀលអង្កាមមានទំនាក់ទំនងជាវិជ្ជមានទៅនឹងកម្រិតកម្ពស់ទឹក និងសីតុណ្ហភាព ហើយជាអវិជ្ជមានជាមួយសារធាតុរ៉ែមួយចំនួន និងកម្រិតទឹកភ្លៀង

ខណៈដែលចំនួនឯកត្តៈនៃប្រភេទត្រីរៀលតុប មានទំនាក់ទំនងជាវិជ្ជមានជាមួយសីតុណ្ហភាព និងកម្រិតសារធាតុចិញ្ចឹមក្នុងទឹក ប៉ុន្តែវាមានទំនាក់ទំនងជាអវិជ្ជមានជាមួយសារធាតុរ៉ែមួយចំនួន។ ជីវម៉ាសរបស់ប្រភេទត្រីទាំងពីរនេះមានទំនាក់ទំនងជាវិជ្ជមានជាមួយនឹងកម្រិតកម្ពស់ទឹក និងសីតុណ្ហភាព ប៉ុន្តែវាមានទំនាក់ទំនងអវិជ្ជមានជាមួយនឹងកម្រិតទឹកភ្លៀង។ ជារួម លទ្ធផលរកឃើញពីការសិក្សារបស់ខ្ញុំអាចជួយដល់ការគ្រប់គ្រងជលផលប្រកបដោយនិរន្តរភាព ដែលមានគោលដៅចូលរួមគាំទ្រដល់ការអភិរក្សប្រព័ន្ធអេកូឡូស៊ី និងសន្តិសុខស្បៀង នៅតំបន់អាងទន្លេមេគង្គក្រោម។

Abstract

Small mud carps (*Henicorhynchus entmema* and *H. siamensis*) are keystone species and commercially important in the Lower Mekong Basin. However, their distribution in space and time is little known within this region. My study was based on high-resolution data collected at 22 sites within the region from 2007 to 2015 and aimed to i) evaluate the abundance and biomass of the two species across the Lower Mekong Basin, ii) explore variation in their populations over time, and iii) investigate the drivers that may determine these patterns. I found that *H. entmema* was abundant in Cambodia (Tonle Sap Lake and river and Mekong mainstream), but much less so in Laos and the Mekong Delta (Vietnam), whereas *H. siamensis* was abundant in the Mekong Delta and Tonle Sap Lake, but less so in the 3S rivers (Cambodia) and Laos. Populations of *H. entmema* declined significantly during the study period in the Tonle Sap Lake, 3S rivers and Mekong mainstream in Cambodia, whereas populations of *H. siamensis* declined at some sites in Vietnam and Cambodia (Tonle Sap Lake). Populations of both species at remaining sites were stable. My results suggest these patterns are regulated by a variety of environmental factors. For instance, the abundance of *H. entmema* was positively associated with water levels and temperature and negatively correlated with certain minerals and precipitation, whereas the abundance of *H. siamensis* was positively correlated with temperature and nutrient levels but negatively associated with certain minerals. The biomass of both species was positively correlated with water levels and temperature, but negatively linked with precipitation. Taken as a whole, my findings can inform sustainable fisheries management aimed at supporting ecosystem conservation and food security within the region.

Household perceptions towards crop-raiding elephants and conservation enterprises: A case study in Prey Proseth village, Ou Bak Roteh Commune, Preah Sihanoukville Province

UNG Chad-Erwan Udom Moni

មូលន័យសង្ខេប

ការសិក្សារបស់ខ្ញុំបានស្វែងយល់ពីការយល់ឃើញរបស់ប្រជាសហគមន៍ចំពោះសត្វដំរីដែលដែលបំផ្លាញដំណាំ និងសហគ្រាសអភិរក្សក្នុងឃុំអូរបាក់រទេះ ខេត្តព្រះសីហនុ ដែលជាទីតាំងមានការអភិវឌ្ឍន៍ផ្លូវថ្នល់ និងការពង្រីកទីលំនៅនិងផ្ទៃដីកសិកម្មរបស់ប្រជាជន ដែលបានជះឥទ្ធិពលដល់ការបំលាស់ទីរបស់សត្វដំរីរវាងជួរភ្នំក្រវាញខាងត្បូង ឧទ្យានជាតិគីរីរម្យនិងបូកគោ។ ដើម្បីសម្រេចបាននូវគោលបំណងនេះ នាខែវិច្ឆិកា ឆ្នាំ២០២០ ខ្ញុំបានសម្ភាស៍ប្រជាពលរដ្ឋចំនួន៩៩គ្រួសារ ដែលរស់នៅក្នុងភូមិព្រៃប្រសិទ្ធ ដើម្បី៖ ១) ស្វែងយល់ពីស្ថានភាពជីវភាពរស់នៅរបស់ពួកគាត់ ២) កំណត់ពីការយល់ឃើញរបស់ពួកគាត់ចំពោះសត្វដំរីដែលបានបំផ្លាញដំណាំនិងសហគ្រាសអភិរក្ស ដើម្បីកាត់បន្ថយជម្លោះរវាងមនុស្ស និងដំរី (HEC) ដែលបានអនុវត្តកន្លងមក ៣) កំណត់កត្តាសេដ្ឋកិច្ចសង្គមដែលទាក់ទងនឹងកិច្ចការទាំងនេះ និង៤) វាយតម្លៃភាពខុសគ្នារវាងគ្រួសារដែលរងផលប៉ះពាល់ដោយសត្វដំរី និងអ្នកដែលមិនបានរងផលប៉ះពាល់ប្រសិនបើមាន។ លទ្ធផលនៃការសិក្សារបស់ខ្ញុំ ជាទូទៅគឺស្របជាមួយនឹងការរកឃើញនៃការសិក្សាកន្លងមក ក្នុងនោះមានទាំងភាពខុសគ្នាជាក់លាក់អំពីយេនឌ័រផងដែរ។ ក្នុងការសិក្សានេះ អ្នកឆ្លើយតបនឹងកំរងសំនួរបានឯកភាពលើសកម្មភាពសំខាន់ៗជាច្រើនក្នុងការកាត់បន្ថយជម្លោះរវាងមនុស្សនិងសត្វដំរី (ជាអាទិភាពគឺការស្តារព្រៃឈើឡើងវិញ និងកម្មវិធីអប់រំផ្សព្វផ្សាយ) និងការអភិវឌ្ឍន៍សហគ្រាសអភិរក្ស។ គ្រួសារដែលរងផលប៉ះពាល់ក្នុងជម្លោះរវាងមនុស្សនិងសត្វដំរីតែងមានទស្សនៈផ្ទុយពីគ្រួសារដែលមិនបានរងផលប៉ះពាល់ចំពោះសកម្មភាពសត្វដំរីដែលបានបំផ្លាញដំណាំ ហើយយេនឌ័រមានឥទ្ធិពលយ៉ាងខ្លាំង

លើទស្សនៈទាក់ទងនឹង HEC។ ការសិក្សានេះក៏បានបង្ហាញជាភ័ស្តុតាងផងដែរពីកិច្ចខិតខំប្រឹងប្រែងកន្លងមកដើម្បីកាត់បន្ថយជម្លោះរវាងមនុស្សនិងសត្វដំរីនៅក្នុងតំបន់នេះ ថាមានឥទ្ធិពលជាវិជ្ជមានទៅលើការយល់ដឹងអំពីការអភិរក្សក្នុងតំបន់។ ជារួមខ្ញុំបានផ្តល់អនុសាសន៍សកម្មភាពមួយចំនួនដើម្បីធ្វើឱ្យប្រសើរឡើងនូវការកាត់បន្ថយជម្លោះរវាងមនុស្សនិងសត្វដំរី និងបង្កើតឱកាសសេដ្ឋកិច្ចសង្គមដើម្បីគាំទ្រដល់កិច្ចការអភិរក្សនៅក្នុងតំបន់។

Abstract

My study explored local perceptions towards crop-raiding elephants and conservation enterprises in the Ou Bak Roteh Commune of Preah Sihanoukville Province, an area where road development and the expansion of human settlements and agriculture have affected the movement of elephants between the Southern Cardamom, Kirirom and Bokor national parks. To achieve this, I interviewed 99 households in Prey Proseth village in November 2020 to i) examine their livelihood circumstances, ii) determine their perceptions towards crop-raiding elephants and past conservation enterprises aimed at mitigating human-elephant conflict (HEC), iii) identify socio-economic factors associated with these, and iv) evaluate if any differences exist between households affected by elephants and those not affected. My results were generally consistent with the findings of previous studies, including gender-specific differences. Study respondents were in general agreement on activities necessary to mitigate HEC (priorities being reforestation and education programmes) and develop conservation enterprises. Households affected by HEC often differed from unaffected households in their views towards crop-raiding elephants and gender had a significant influence on views regarding HEC. It was also evident that previous efforts to mitigate HEC in the area have had a positive effect on local conservation awareness. I conclude by recommending several actions to expand HEC mitigation and develop socio-economic opportunities to further support conservation in the area.

Recent literature from Cambodia

This section summarizes recent scientific publications concerning Cambodian biodiversity and natural resources. The complete abstracts of most articles are freely available online (and can be found using Google Scholar or other internet search engines), but not necessarily the whole article. Corresponding authors may be willing to provide free reprints or electronic copies on request and their email addresses, where known, are included in the summaries below.

Documents that use the Digital Object Identifier (DOI) System can be opened via the website http://dx.doi.org (enter the full DOI code in the text box provided and click Go to find the document).

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New species & taxonomic reviews

Csorba, G. & Furey, N.M. (2022) From greener times: a new species of thick-thumbed Myotis from Phnom Penh, Cambodia. *Acta Zoologica Academiae Scientiarum Hungaricae*, **68**, 85–97.

The authors describe a new species of mouse-eared bat to science (*Myotis hayesi* sp. nov) based on a single specimen collected in Phnom Penh in 2000. The new species is characterized by its fleshy, bicoloured thumb, large foot sole, full dentition, relatively short rostrum, and high frontal part of the skull. Author: neil.m.furey@gmail.com

Gupta, S.K., Kumar, A., van Berkel, T., Emsens, W.-J., Singh, B., Puls, S., Rin N. & Jocque, M. (2022) Genetic analysis reveals a distinct lineage of hog deer (*Axis porcinus*) in Kratie province, Cambodia. *Journal of Heredity*. DOI 10.1093/jhered/esac017

Two subspecies of hog deer are currently recognised: *A. p. porcinus*, ranging from Punjab Province in Pakistan, Nepal and the northern part of India to Myanmar, and *A. p. annamiticus*, occurring in Indochina, Thailand, Laos, Cambodia and Vietnam. The authors analysed variation in the mitochondrial DNA control region of samples of the latter subspecies from Kratie Province and found that these differ from mainland Indian and Thai populations. They conclude that the population in Kratie appears to be a distinct lineage which should be treated as an evolutionarily significant unit. Author: skg@wii.gov.in

Kosterin, O. (2021) *Burmagomphus williamsoni eddiei* subsp. nov. (Odonata, Gomphidae) from northern Cambodia. *International Dragonfly Fund-Report*, **161**, 1–15.

The author describes a new subspecies of dragonfly to science based on specimens collected in Phnom Kulen (Siem Reap Province) in 2018. The new subspecies also occurs in Preah Vihear Province. Author: kosterin@bionet.nsc. ru

Nekaris, K.A.-I. & Nijman, V. (2022) A new genus name for pygmy lorises, *Xanthonycticebus* gen. nov. (Mammalia, Primates). *Zoosystematics and Evolution*, **98**, 87–92.

Several studies have suggested that marked differences between the pygmy slow loris *Nycticebus pygmaeus* and other *Nycticebus* species may warrant recognition at the generic level. Based on morphological, behavioural, karyotypical and genetic data, the authors show that these differences are significant and consistent and propose *Xanthonycticebus* gen. nov. as a new genus name for pygmy slow lorises. They also indicate that their nomenclatural changes should not affect the legal status of species presently recognised. Author: vnijman@brookes.ac.uk

Souladeth, P., Newman, M.F. & Prajaksood, A. (2022) Two new species of *Eriocaulon* (Eriocaulaceae) from Cambodia. *Kew Bulletin*, **77**, 127–137.

The authors describe two new species of *Eriocaulon* from Bokor National Park in Kampot Province: *E. bokorense* and *E. cambodianum*. A conservation assessment based on IUCN guidelines is also provided for each species. Author: amopra@kku.ac.th

Stuart, B.L. & Rowley, J.J.L. (2020) A new *Leptobrachella* (Anura: Megophryidae) from the Cardamom Mountains of Cambodia. *Zootaxa*, **4834**, 556–572.

The authors describe a new species of frog to science (*Leptobrachella neangi* sp. nov) based on morphological and genetic analyses of two specimens collected in the Cardamom Mountains. The new species is readily distinguished from its congeners by morphological features and is the third species of *Leptobrachella* confirmed in Cambodia. Author: bryan.stuart@naturalsciences.org

Vuong T.T., Görföl, T., Csorba, G., Arai S., Kikuchi F., Fukui D., Koyabu D., Furey, N.M., Saw Bawm, Kyaw San Lin, Alviola, P., Chu T.H., Nguyen T.S., Tran A.T. & Hassanin, A. (2021) Integrative taxonomy and biogeography of Asian yellow house bats (Vespertilionidae: *Scotophilus*) in the Indomalayan Region. *Journal of Zoological Systematics and Evolutionary Research*. DOI 10.1111/jzs.12448

The authors integrate morphological and molecular analyses to clarify the taxonomic status and phylogeographical patterns of yellow house bats (*Scotophilus*), a widespread genus of vespertilionid bats in the Indomalayan Region. Their results show these can be classified into just two widespread species, namely the smaller *S. kuhlii* and the larger *S. heathii*, which occur in sympatry in different parts of Southeast Asia, including Cambodia. Author: vttu@iebr.ac.vn

Yooprasert, S., Culham, A., Tagane S., Yahara T., Nguyen V.D., Nguyen K.S. & Utteridge, T.M.A. (2022) New species and new status of *Urophyllum* Wall. (Rubiaceae) from Cambodia and Viêtnam. *Adansonia*, **44**, 91–114.

The authors describe five new species of *Urophyllum* which are endemic to Cambodia and Vietnam. An identification key is provided for *Urophyllum* species in Cambodia, Laos and Vietnam and point occurrence maps are also presented for each species, as well as conservation assessments based on IUCN guidelines. Author: saveta.yo@gmail.com

Biodiversity inventories

Capelle, J., Furey, N., Hoem T., Ou T.P., Lim T., Hul V., Heng O., Chevalier, V., Dussart, P. & Duong V. (2021) Longitudinal monitoring in Cambodia suggests higher circulation of alpha and betacoronaviruses in juvenile and immature bats of three species. *Scientific Reports*, **11**, 24145.

Recent studies suggest that the progenitors of the SARS-CoV-2 virus could have originated in rhinolophid bats within the region. The authors sampled bats in Cambodia to test the association between their age and CoV infection status and reviewed the literature to determine the reproductive phenology of bat genera in southeast China, Vietnam, Laos and Cambodia. Their results suggest an association between positive coronavirus detections and juvenile and immature bats in Cambodia. As literature review indicates reproduction is largely synchronised among rhinolophid and hipposiderid bats, they suggest surveillance of CoV in insectivorous bat species in Southeast Asia could target certain months of year to maximise detection probabilities. Author: julien.cappelle@cirad.fr

Furey, N.M., Vuong T.T., Hitch, A., Pimsai, A., Chor K., Buor V., Yim R., Chheang S., Borthwick, S.A., Ch'ng L., Say S., Csorba, G., Ith S., Smith, G.J.D., Chheang D. & Mendenhall, I. (2021) First records of seemingly rare bats (Mammalia: Chiroptera) in Cambodia, with a revised checklist of species for the country. *Acta Chiropterologica*, **23**, 345–369.

Based on field surveys undertaken throughout Cambodia in 2014–2020, the authors use morphological, genetic and acoustic data to document the first records of six bat species nationally (*Rhinolophus marshalli*, *R. siamensis*, *Hipposideros halophyllus*, *H. lekaguli*, *Cassistrellus yokdonensis* and *Eptesicus pachyomus*) and the second in-country record for one additional species (*Saccolaimus saccolaimus*). They also provide a revised checklist of the 80 bat species now confirmed in Cambodia and remark on the potential for additional discoveries. Author: neil.m.furey@gmail.com

Kosterin, O. (2020) First data on Odonata of Prey Long Forest in Cambodian lowland. *International Dragonfly Fund-Report*, **154**, 1–27.

Kosterin, O. (2020) Odonata of the great Lake Tonle Sap of Cambodia, as examined in 2017–2019. *International Dragonfly Fund-Report*, **154**, 29–98.

Kosterin, O. & Smith, E. (2020) Odonata of Phnom Kulen Mts, Cambodia: a preliminary checklist. *International Dragonfly Fund-Report*, **154**, 99–183.

Kosterin, O. (2020) Miscellaneous faunal data on Odonata of Cambodia. *International Dragonfly Fund-Report*, **154**, 185–223.

A series of papers documenting Odonata (dragonflies and damselflies) present in the vicinity of Prey Long, Tonle Sap Lake, Phnom Kulen, Siem Reap Province, Phnom Tbeng, Mondulkiri Province and Pursat Province. These include checklists of species for the studied localities and the first records for multiple taxa in Cambodia. Author: kosterin@bionet.nsc.ru

MacGowan, I. & Barták, M. (2022) An annotated list of Lonchaeidae (Diptera) from China, Cambodia and Vietnam with description of a new species. *Far Eastern Entomologist*, **447**, 10–16.

The authors provide a preliminary checklist of 14 species within the Lonchaeidae occurring in Cambodia, China and Vietnam. These include two species in Cambodia: *Silba ischnopoda* and *S. setifera*. Author: imacgowan9@gmail.com

Pin C., Kamler, J.F., Toem Y., Lay D., Vorn K., Kim N. & Macdonald, D.W. (2022) First record of a giant muntjac *Muntiacus vuquangensis* (Cervidae) from Cambodia. *Mammalia*. DOI 10.1515/mammalia-2021-0132

The giant muntjac *Muntiacus vuquangensis* is a Critically Endangered ungulate whose distribution extends along the Annamite Mountains in Laos and Vietnam. Based on a camera trap image taken in Virachey National Park, the authors report the first confirmed record of the species in Cambodia and suggest this likely represents an isolated population near the western edge of the species' distribution. Author: chanratana.pin@gmail.com

Si N., Ader, D. & Srean P. (2021) A checklist of wild orchids in Battambang, Cambodia. *Asian Journal of Agricultural and Environmental Safety*, **2021**, 66–68.

The authors report the occurrence of 79 species of wild orchids belonging to 38 genera in Battambang Province. Author: pao.srean@gmail.com

Zhang C., Luo C., Yang R., Yang Y., Guo X., Deng Y., Zhou H. & Zhang Y. (2022) Morphological and molecular identification reveals a high diversity of *Anopheles* species in the forest region of the Cambodia–Laos border. *Parasites & Vectors*, **15**, 94.

The authors employed morphological and molecular techniques to identify 2,394 mosquitoes collected in Siem Pang (Cambodia) and Pathoomphone (Laos). They identified 13 species of *Anopheles* in this region, with dominant species including *A. dirus*, *A. maculatus*, *A. philippinensis*, *A. kochi* and *A. sinensis*. Author: jamesyilong1010@aliyun.com

Species ecology & status

Freund, D., Signs, M. & Yoganand, K. (2021) *Primates of the Greater Mekong: Status, Threats and Conservation Efforts*. World Wide Fund for Nature, Gland, Switzerland. Https://wwfasia.awsassets.panda.org/downloads/primate_report_final_optimized.pdf [Accessed 3 June 2022].

Forty-four non-human primate species are currently recognised in the Greater Mekong region, some of which only occur in a single country or a small part of a country. This report summarizes the status of and threats to primates in the region and efforts by government and non-government agencies to conserve these. Despite the latter efforts, the authors conclude that many species are seriously threatened due to loss and fragmentation of habitats, coupled with poaching and trade of primates for meat, traditional medicine and pets.

Gray, T.N.E., Belecky, M., O'Kelly, H.J., Rao, M., Roberts, O. Tilker, A., Signs, M. & Yoganand, K. (2021) Understanding and solving the South-East Asian snaring crisis. *The Ecological Citizen*, **4**, 129–141.

The increasing use of snares for wildlife hunting is a major cause of population declines in terrestrial species in Southeast Asia. The authors document the removal of 371,056 snares from 11 protected areas in the region between 2005 and 2019. Due to the low detectability of snares and large size of many of the protected areas, this is believed to be a small fraction of total snares present. To address the threats posed by snares, anti-poaching patrols need urgent improvement and legislative changes are required to allow law enforcement officers to deter snaring in protected areas. Evidence-based campaigns to reduce the commercial demand for wildlife meat are also required. Author: tgray@wwf-tigers.org

Kamler, J.F., Minge, C., Rostro-García, S., Gharajehdaghipour, T., Crouthers, R., In, V., Pay C., Pin C., Sovanna P. & Macdonald, D.W. (2021) Home range, habitat selection, density, and diet of golden jackals in the Eastern Plains Landscape, Cambodia. *Journal of Mammalogy*, **102**, 636–650.

The authors used radio and GPS collars to evaluate movements and habitat selection of golden jackals *Canis aureus* in dry deciduous forest in Srepok Wildlife Sanctuary. They also analysed 147 scats to determine seasonal variation in diets and prey selection. The mean annual size of home ranges was considerably larger than previously reported and resulted in an extremely low density. Jackals avoided dense forests and streams and had a strong selection for dirt roads, possibly to avoid larger predators. The diet was diverse in including at least 16 prey items, with no significant differences between seasons. The authors suggest jackals are an extremely adaptable and opportunistic species that exhibit unique behaviours to survive near the edge of their distribution. Author: jan.f.kamler@gmail.com

Ladd, R., Crouthers, R., Brook, S. & Eames, J.C. (2022) Reviewing the status and demise of the Endangered Eld's deer and identifying priority sites and conservation actions in Cambodia. *Mammalia*. DOI 10.1515/mammalia-2021-0151

Eld's deer *Rucervus eldii* once occurred widely across Southeast Asia, but is now listed as Endangered, having suffered severe population declines and range contractions. The authors assess its status in Cambodia based on records between 2000 and 2020 and conclude that very small, isolated populations of the species are now mostly restricted to nine areas in the eastern and northern parts of the country. They also suggest that urgent conservation actions including effective law enforcement and anti-hunting strategies are required to ensure survival of the species in Cambodia. Author: r.ladd@uq.net.au.

McGrath, S.J. & Behie, A.M. (2021) Hunting pressure on primates in Veun Sai-Siem Pang National Park, Cambodia. *International Journal of Primatology*. DOI 10.1007/s10764-021-00219-1

Six primate species are known to inhabit Veun Sai-Siem Pang National Park in northeast Cambodia. The authors investigated hunting pressure on these by interviewing 96 people in five villages adjacent to the park. Their results suggest that pygmy slow loris *Nycticebus pygmaeus* is the most frequently hunted, sold and sought-after primate species within the national park and is used in traditional medicine. Additionally, the northern yellow-cheeked crested gibbon *Nomascus annamensis* is most sought after for use as a pet, although this species is reportedly only rarely caught within the park. Author: sarah.mcgrath@anu.edu.au

Nuttall, M.N., Griffin, O., Fewster, R.M., McGowan, P.J.K., Abernethy, K., O'Kelly, H., Nut M., Sot V. & Bunnefeld, N. (2021) Long-term monitoring of wildlife populations for protected area management in Southeast Asia. *Conservation Science and Practice*. DOI 10.1111/csp2.614

Although rare, long-term monitoring of biodiversity in protected areas is critical to assess threats, link conservation actions to species outcomes and improve management. Based on line transect distance sampling surveys in Keo Seima Wildlife Sanctuary between 2010 and 2020, the authors report abundance estimates and population trends for 11 species and spatial distributions for seven species. Their results indicate arboreal primates and green peafowl *Pavo muticus* generally had either stable or increasing population trends, whereas ungulates and semi-arboreal primates generally had declining trends. This suggests that ground-based threats, such as snares and domestic dogs, are having serious negative effects on terrestrial species. Author: mattnuttall00@gmail.com

Pin C., Phan C., Kamler, J.F., Rostro-García, S., Penjor, U., In, V., Crouthers, R., Macdonald, E.A., Chou S. & Macdonald, D.W. (2022) Density and occupancy of leopard cats across different forest types in Cambodia. *Mammal Research*. DOI 10.1007/s13364-022-00634-6

The leopard cat *Prionailurus bengalensis* is the most common wild felid in Southeast Asia, yet little is known about the factors that affect their population density and occupancy of natural habitats. The authors used camera trap surveys to determine densities of leopard cats in three forest types in Cambodia and conducted occupancy analyses to evaluate their interactions with leopards *Panthera pardus*, dholes *Cuon alpinus* and domestic dogs *Canis familiaris*. Estimated densities were highest in continuous evergreen forest, followed by mosaics dominated by evergreen forest and mosaics dominated by dry deciduous forests. The probability of occupancy for leopard cats was not affected by the presence or absence of any large carnivore. The authors suggest their findings support the notion that leopard cats are habitat generalists, although evergreen forest appears to be the optimum natural habitat for the species in Southeast Asia. Author: chanratana.pin@gmail.com

Phun T., Platt, S.G., Som S. & Rainwater, T.R. (2021) *Crocodylus siamensis* (Siamese crocodile). Attempted predation. *Herpetological Review*, **52**, 400–401.

This note reports observations of attempted predation of a small juvenile Siamese crocodile by a snakehead fish (*Channa* sp.) in the Sre Ambel River System of Koh Kong Province in 2020. Author: pthorn@wcs.org

Rostro-García, S., Kamler, J.F., Minge, C., Caragiulo, A., Crouthers, R., Groenenberg, M., Gray, T.N.E., In, V., Pin C., Sovanna P., Kery, M. & Macdonald, D.W. (2021) Small cats in big trouble? Diet, activity, and habitat use of jungle cats and leopard cats in threatened dry deciduous forests, Cambodia. *Ecology and Evolution*. DOI 10.1002/ece3.7316

The jungle cat *Felis chaus* is a little known dry deciduous dipterocarp forest (DDF) specialist that only occurs in small isolated populations in Southeast Asia. The authors used camera trap data and DNA-confirmed scats collected in Srepok Wildlife Sanctuary from 2009 to 2019 to determine temporal, dietary and spatial overlap between jungle cats and the more common leopard cats *Prionailurus bengalensis*. The diet of jungle cats was more diverse than leopard cats, although both species mostly consumed small rodents. Both species were primarily nocturnal and had high temporal overlap, although modelling suggested jungle cats were restricted to DDF and had low occupancy, whereas leopard cats had higher occupancy and were habitat generalists. The former suggests protection of large areas of DDF will be required to conserve jungle cats in Southeast Asia. Author: rostro.susana@gmail.com

Schloesing, E., Chambon, R., Tran A., Choden, K., Ravon, S., Epstein, J.H., Hoem T., Furey, N., Labadie, M., Bourgarel, M., De Nys, H.M., Caron, A. & Cappelle, J. (2020) Patterns of foraging activity & fidelity in a Southeast Asian flying fox. *Movement Ecology*, **8**, 46.

The authors analysed GPS data obtained from eight *Pteropus lylei* to evaluate the influence of environmental and behavioral variables on their foraging patterns in a heterogeneous landscape in Cambodia. The bats performed few foraging bouts (area-restricted searches) on a given night, mainly in residential areas, and the duration of these decreased during the night. The probability of a bat revisiting a foraging area within 48 hrs varied according to the time previously spent there, its distance from the roost site, and the corresponding habitat type. The study provides evidence that human-made environments may promote complex patterns of foraging-behaviour and short-term re-visitation in fruit bat species within these landscapes. Author: elodie.schloesing@gmail.com

Som S., Platt, S.G., Haislip, N.A. & Rainwater, T.R. (2021) *Cyclemys atripons* (black-bridged leaf turtle). Reproduction. *Herpetological Review*, **52**, 389–390.

The authors describe the eggs and reproductive phenology of *C. atripons* in Cambodia, based on observations of a female obtained near Peam Krasaop Wildlife Sanctuary and temporarily held at the Koh Kong Reptile Conservation Center. Author: ssom@wcs.org

Tak C., Crouthers, R., Sukumal, N., Chhin S. & Savini, T. (2022) Importance of Srepok Wildlife Sanctuary, Cambodia, for the endangered green peafowl: implications of co-occurrence near human use areas. *Raffles Bulletin of Zoology*, **70**, 249–256

The Endangered green peafowl *Pavo muticus* has dramatically declined in recent decades, with northern and eastern Cambodia representing one of the few remaining strongholds for the species. The authors conducted distance-based point counts of vocalisations to estimate densities of male green peafowls in Srepok Wildlife Sanctuary during the 2016 breeding season. This resulted in an estimated population of 1,165 calling males. Compared to the core survey area, densities of males were higher in the outer survey area, and closer to human settlements and agricultural farms. The authors recommend that future conservation initiatives incorporate holistic approaches to integrate the needs of people and wildlife in areas of shared resources. Author: rachel.crouthers1@gmail.com

van Berkel, T., Emsens, W.-J., Eam S.U., Simoes, S., Puls S., Rin N., Kimsan L. & Jocque, M. (2022) Population density, habitat use and activity patterns of endangered hog deer in Cambodia. *Mammal Research*. DOI 10.1007/s13364-022-00619-5

Hog deer *Axis porcinus* were once widespread throughout much of lowland Southern Asia, but have rapidly declined in the last two decades. The authors conducted two camera trap surveys of a recently discovered population along the western bank of the Mekong River, near Kratie. They found that hog deer were confined to a ca. 2 km^2 relict patch of tall moist grassland during the dry season and estimated a density of 41.8 individuals/km^{-2}. Activity was mainly crepuscular and nocturnal. They conclude that the population (with an estimated 84 individuals) is extremely vulnerable to extinction due to its small size and dependency on a tiny remnant patch of core habitat. Author: info@binco.eu

Coasts, wetlands & aquatic resources

Sor R., Ngor P.B., Soum S., Chandra S., Hogan, Z.S. & Null, S.E. (2021) Water quality degradation in the Lower Mekong Basin. *Water*, **13**, 1555.

As one of the largest rivers in the world, the Mekong River supports significant biodiversity and ecosystem services. Based on biological and physical-chemical data collected over the last two decades, the authors employed biotic and abiotic metrics to evaluate water quality within the Lower Mekong Basin (LMB). Their results suggest water quality declined in the LMB in the 2010s, particularly near Vientiane City, the Sekong, Sesan, and Srepok Rivers, Tonle Sap Lake and Mekong Delta. This decline is likely associated with flow alteration, erosion, sediment trapping and point and non-point wastewater, which have resulted from rapid hydropower development, deforestation, intensive agriculture, plastic pollution and urbanization in the region. Author: sorsim.ratha@gmail.com

Strong, J.A., Wardell, C., Haïssoune, A., Jones, A.L. & Coals, L. (2022) Marine habitat mapping to support the use of conservation and anti-trawl structures in Kep Province, Cambodia. *ICES Journal of Marine Science*. DOI 10.1093/icesjms/fsac001

Despite designation as a Marine Fisheries Management Area (a local form of marine protected area), illegal trawling has continued to damage vulnerable marine habitats within the Kep Archipelago. The authors deployed 40 conservation and anti-trawling structures within the archipelago which can snare nets used by illegal trawlers and provide substrates for coral colonization. They present the results of a side-scan sonar survey and ground truthing campaign used to precisely locate these structures and produce maps of the important benthic habitats in the area. Author: james.strong@noc.ac.uk

Forests & forest resources

Crouthers, R. (2021) *Human Wildlife Interactions and People's Perceptions Towards Wildlife, Conservation and Protected Area Management Systems Across Communities Living Within or Adjacent to Srepok and Phnom Prich Wildlife Sanctuaries*. World Wide Fund for Nature, Phnom Penh, Cambodia.

This technical report presents the results of 1,369 household interviews undertaken in 49 villages located within and adjacent to the Srepok and Phnom Prich wildlife sanctuaries in eastern Cambodia. The overall purpose of the surveys was to generate baseline information to facilitate the future development of interdisciplinary conservation strategies within the area. Author: rachel.crouthers1@gmail.com

Ehara M., Saito H., Michinaka T., Hirata Y., Leng C., Matsumoto M. & Riano, C. (2021) Allocating the REDD+ national baseline to local projects: a case study of Cambodia. *Forest Policy and Economics*, **129**, 102474.

The authors evaluate forest cover, forest carbon stocks and historical deforestation trends using 77 hypothetical REDD+ (Reducing Emissions from Deforestation and forest Degradation) projects and five actual REDD+ projects in Cambodia. These analyses are employed to propose tools for deciding Cambodia's national REDD+ baseline or initial forest reference level for local REDD+ projects. Author: makotoehara1@gmail.com

The Recent Literature section was compiled by Neil Furey, with contributions from Oleg Kosterin.

Instructions for Authors

Purpose and Scope

The *Cambodian Journal of Natural History* (ISSN 2226–969X) is an open access, peer-review journal published biannually by the Centre for Biodiversity Conservation at the Royal University of Phnom Penh. The Centre for Biodiversity Conservation is a non-profit making unit, dedicated to training Cambodian biologists and the study and conservation of Cambodia's biodiversity.

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The following types of manucripts are accepted:

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- Letters to the editor (<650 words)

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Full Papers (2,000–7,000 words, excluding references) and Short Communications (300–2,000 words, excluding references) are welcomed on topics relevant to the Journal's focus, including:

- Research on the status, ecology or behaviour of wild species.
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- Discoveries of new species records or range extensions.
- Reviews of conservation policy and legislation in Cambodia.
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Concise reports (<300 words) on news of general interest to the study and management of Cambodia's biodiversity. News items may include, for example:

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Informative contributions (<650 words), usually in response to material published in the Journal.

Recent Literature

Copies or links to recent (<18 months) scientific publications concerning Cambodian biodiversity and the management of natural resources. These may include journal papers, project technical reports, conference posters and student theses.

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Preparation of Manuscripts

Authors should consult previous issues of the journal for general style, and early-career authors are encouraged to consider guidance provided by:

Fisher, M. (2012) Editorial—To shed light on dark corners. *Cambodian Journal of Natural History*, **2012**, 1–2.

Daltry, J.C., Fisher, M. & Furey, N.M. (2012) Editorial – How to write a winning paper. *Cambodian Journal of Natural History*, **2012**, 97–100.

Manuscripts should be in English and use UK English spelling (if in doubt, Microsoft Word and similar software should be set to check spelling and grammar for 'English (UK)' language). Lines should be double-spaced. Submissions can be in 'doc', 'docx' or 'rtf' format, preferably as a single file attached to one covering email.

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Title: A succinct description of the work, in no more than 20 words.

Abstract: (Full papers only). This should describe, in no more than 250 words, the aims, methods, major findings and conclusions. The abstract should be informative and intelligible without reference to the text, and should not contain any references or undefined abbreviations. Cambodian authors are strongly encouraged to submit a Khmer translation of the English abstract.

Keywords: (Full papers only). Up to eight pertinent words, in alphabetical order.

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Main text: (Full papers). This should comprise the following sections in order: Introduction, Methods, Results, Discussion and Acknowledgements. Subsections may be included in the Methods, Results and Discussion sections if necessary. Conclusions and recomendations should be included in the Discussion.

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Tanaka S. & Ohtaka A. (2010) Freshwater Cladocera (Crustacea, Branchiopoda) in Lake Tonle Sap and its adjacent waters in Cambodia. *Limnology,* **11,** 171–178.

Books and chapters:

Khou E.H. (2010) *A Field Guide to the Rattans of Cambodia.* WWF Greater Mekong Cambodia Country Programme, Phnom Penh, Cambodia.

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

Rawson, B. (2010) The status of Cambodia's primates. In *Conservation of Primates in Indochina* (eds T. Nadler, B. Rawson & Van N.T.), pp. 17–25. Frankfurt Zoological Society, Frankfurt, Germany, and Conservation International, Hanoi, Vietnam.

Reports:

Lic V., Sun H., Hing C. & Dioli, M. (1995) *A Brief Field Visit to Mondolkiri Province to Collect Data on Kouprey* (Bos sauveli), *Rare Wildlife and for Field Training.* Unpublished report to Canada Fund and IUCN, Phnom Penh, Cambodia.

Theses:

Yeang D. (2010) *Tenure rights and benefit sharing arrangements for REDD: a case study of two REDD pilot projects in Cambodia*. MSc thesis, Wageningen University, Wageningen, The Netherlands.

Websites:

IUCN (2010) *2010 IUCN Red List of Threatened Species.* Http://www.redlist.org [accessed 1 December 2010].

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