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Leaf Traits on the Bokor Plateau

Rewilding in Western Siem Pang

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Cover image: Banteng *Bos javanicus*, Thporng District, Kampong Speu Province, 21 April 2019 (© J.C. Eames). The prospects for rewilding in northeastern Cambodia through this and other globally threatened species is reviewed in the present issue by Gray *et al*. (pages 98–112).

Leaf traits in the dwarf montane heathland of the Bokor Plateau, Cambodia

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មូលន័យសង្ខេប

ភាពគ្របដណ្តប់ដោយពពកជាញឹកញាប់ រួមជាមួយនឹងរបបទឹកភ្លៀងកម្រិតខ្ពស់ និងខ្យល់ខ្លាំង ផ្សំជាមួយកត្តាប្រភេទដីថ្មភក់ (sandstone soils) ដែលមានកម្រិតអាស៊ីតទាបនៅលើតំបន់ខ្ពង់រាបបូកគោនៃជួរភ្នំដំរី វាបង្កើតឱ្យមានលក្ខខណ្ឌកំណត់មួយដែលធ្វើមាននូវប្រភេទព្រៃក្រិននៃតំបន់ភ្នំត្រូពិក។ វាមានកម្ពស់ដើមឈើខុសគ្នាខ្លាំង គឺពី២០-៣០ម៉ែត្រ សម្រាប់ព្រៃរងទឹកភ្លៀងនៅតាមទីជម្រាលភ្នំ និងបន្ទាប់មកជាប្រភេទព្រៃឈើដែលមានកម្ពស់ទាបៗ និងចុងក្រោយគឺមានពពួករុក្ខជាតិក្រិនស្លឹករឹង កម្ពស់ពី ៣-៤ម៉ែត្រ (sclerophyll heathland) មានវត្តមាននៅលាយឡំជាមួយពពួកដើមឈើទាបៗ (shrub canopy matrix)។ លក្ខណៈរូបសាស្ត្រនៃទំហំនិងទម្ងន់ស្លឹក លក្ខណៈរស្មីសំយោគនៃមធ្យមអតិបរមានៃអត្រាសម្រូប(assimilation rate) រួមជាមួយនឹងប្រសិទ្ធភាពនៃការប្រើប្រាស់ទឹក ($\delta^{13}C$) គឺមានភាពខុសគ្នារវាងពពួករុក្ខជាតិក្រិន និងពពួកដើមឈើទាបៗ (ទាំង woody shrubs និងlow-stature colonizing shrubs) នូវលក្ខណៈតែមួយគឺភាពមានទំហំស្លឹកធំជាប់លាប់។ ខ្សែកោងឆ្លើយតបទៅនឹងលក្ខខណ្ឌពន្លឺបានបង្ហាញឱ្យឃើញថា ជម្រាបឆ្អែតនៃថាមពលពន្លឺ (saturating irradiance) កើតមាននៅចន្លោះពី៤០០-៥០០μmol m^{-2} s^{-1} គឺតិចជាង១/៤នៃពន្លឺព្រះអាទិត្យ(full sun)។ ទោះបីជាពេលរសៀលហាក់ដូចជាលក្ខខណ្ឌប្រសើរសម្រាប់ធ្វើរស្មីសំយោគ ប្រភេទរុក្ខជាតិដែលបានសិក្សានោះតែងបង្ហាញលក្ខណៈបិទស្តូម៉ាតជាញឹកញាប់ និងបន្ទាបកម្រិតអត្រាស្រូបពន្លឺរបស់វារហូតដល់តម្លៃជាអវិជ្ជមាន។

Abstract

The frequent cloud cover and associated high levels of rainfall and strong winds combined with shallow acidic sandstone soils on the Bokor Plateau of the Elephant Mountains produce classic limiting conditions that lead to the formation of a dwarf tropical montane forest. Tree stature grades quickly from rainforest canopies 20–30 m in height on sheltered slopes, to lower stunted forest, and finally to a low sclerophyll heathland with scattered dwarfed treelets 3–4 m in height in a low shrub canopy matrix. Leaf morphological traits of size and specific leaf weight, photosynthetic traits of mean maximum assimilation rate and integrated water use efficiency ($\delta^{13}C$) differed between dwarfed treelets and both woody shrubs and low-stature colonizing shrubs in only the single trait of having consistently larger leaves. Light response curves showed that saturating irradiance occurred at 400–500 μmol m^{-2} s^{-1}, less than one quarter of full sun. Despite seemingly favourable conditions for photosynthesis in the afternoon, study species frequently exhibited stomatal closure and low to even negative rates of net assimilation.

Keywords Bokor National Park, dwarf forest, heathland, leaf traits, tropical mountain cloud forest.

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Introduction

Tropical montane cloud forests, characterized by the persistent presence of mist or low clouds that result in deposition of water on the vegetation, are widespread throughout tropical regions of the world (Hamilton *et al*., 1995; Aldrich *et al*., 1997). These forests are typically low in stature with slow growth and are commonly described as dwarf forests. Their low stature and associated slow rates of growth have been attributed to a complex interaction of diverse potential limiting factors. These include cloud cover that reduces solar radiation levels for photosynthesis, relatively low ambient air temperatures, strong winds, high rainfall that leaches soils and slows rates of mineralization and decomposition, and limited nutrient availability (Bruijnzeel & Proctor, 1995; Tanner *et al*., 1998; Bruijnzeel & Veneklaas, 1998; Bruijnzeel *et al*., 2011).

Examples of tropical montane cloud forests can be seen in southern Cambodia in the Cardamom and Elephant Mountains where proximity to the Gulf of Thailand brings unusually high levels of rainfall (Daltry & Momberg, 2000; Rundel *et al*., 2016). These mountain ranges are largely Mesozoic sandstone, with localized areas of limestone and volcanic rock. Acid lithosols develop over the sandstone parent material that characterizes much of the Elephant Mountains. These thin acidic soils are heavily leached by the high rainfall and easily eroded in disturbed conditions.

The weathered Bokor Plateau exhibits a classic example of a tropical montane cloud forest with dwarf trees. As the plateau slopes gently over a linear distance of about 4 km from near Popokvil Waterfall (920 m) southwards towards the coastal escarpment at the old Bokor Hotel (1,062 m), rainforest canopies 20–30 m in height first give way to a stunted forest 10–15 m in height, and finally to a low sclerophyllous heathland with scattered dwarfed treelets 3–4 m in height in a low shrub canopy matrix of only 1–2 m. Dy Phon (1970) termed this *la lande de myrtacées et vacciniacées* because of the dominance of these two families.

While the flora of the plateau has distinct elements (Rundel *et al*., 2017), many forest tree species occur on both the upper mountain slopes and the plateau itself, providing an opportunity for comparative studies. The gradient in growing conditions has been described for the canopy dominant *Dacrydium elatum* (Roxb.) Wall. ex Hook.f across the plateau. Trees near the Popokvil Waterfall are 14–16 m in height, drop to 8–10 m across the plateau, and finally reach only 4–6 m to the south near the coastal escarpment (Rundel *et al*., 2016).

Our objective in this study was to investigate comparative patterns of leaf morphological and ecophysiological traits in a group of 19 woody species growing near the coastal escarpment of the Bokor Plateau where high rainfall and shallow heavily weathered soils produce dwarfing conditions for forest trees. Our study species included monopodial treelets dwarfed from their normal canopy height, shrubby taxa of intermediate height, and low-growing shrubs that colonize open sites (Table 1). We looked for traits that might be associated with the dwarfed tree species and help explain their slow growth. An additional objective was to use measurements of net photosynthetic assimilation to establish the maximum rates present and potential role of heavy cloud cover and reduced irradiance in limiting photosynthesis.

Field Site and Methods

Study site and species

Field studies were carried out from 3–13 March 2001 on the Bokor Plateau of the Elephant Mountains in Bokor National Park, Kampot Province, Cambodia. Bokor National Park was established in 1997 and covers an area of 140,000 ha (Rundel *et al*., 2003; Tagane *et al*., 2017). Our measurements took place about 0.8–1.0 km north of the old hotel in sclerophyllous heathland habitat. The sandstone substrate of this area of the plateau was heavily weathered with shallow rocky soil and fracture lines forming soil pockets of coarse acidic white sand. Soil pH was 4.7.

Rainfall is extremely high on the Bokor Plateau, averaging more than 5,000 mm annually. Records for Bokor (950 m elevation) at the southern end of the plateau show a mean annual rainfall of 5,309 mm (Tixier, 1979), while the Val d'Emeraude on the southeast margin of the plateau receives a mean rainfall of 5,384 mm (Dy Phon, 1970). The distribution of this rain, however, is strongly seasonal, peaking in July and August. These stations have been reported to receive an average of 170 and 223 days a year of rainfall, respectively (Anonymous, 1979). The dry season at these stations is restricted to 2–3 months from December through February and rainfall drops to 50 mm or less in January and February at both stations. The Val d'Emeraude experiences rain almost every day from May through October, but on only 12 days on average in March (Dy Phon, 1970), the month of our sampling. Mornings during our field studies were typically semi-sunny with scattered clouds moving overhead, while heavier overcast conditions and brief periods of intense rain occurred almost every afternoon. Mean monthly temperatures are relatively constant throughout the year at Bokor, varying only from a low of 19.2°C in July and August to a high of 21.5°C in April (Dy Phon, 1970).

Leaf trait analyses

Our study species were characterized as treelets with a single main stem, shrubs with a branched form of canopy architecture, or low shrubs with a low to prostrate growth form. Mean height was measured and compared to maximum heights at favourable forest sites as indicated in the literature. Examples of leaf morphology for four of our study species are shown in Fig. 1. Samples of three leaves from each of three individual plants for each study species were collected for measurement of leaf morphological traits and these represented the youngest fully mature leaf on an actively growing branch. Foliar areas were measured on fresh leaves using a LI-COR portable leaf area meter (LI-COR Inc., Lincoln, Nebraska, USA), then archived for dry weight measurements in a laboratory. Specific leaf weight was calculated as the leaf dry weight per unit area.

Stable carbon isotope ratios of ^{13}C and ^{12}C ($\delta^{13}C$) provide a measure of integrated water use efficient over the period in which carbon was used in leaf construction. Values are negative with lower (more negative) values indicating low water use efficiency while less negative numbers indicate higher water use efficiency (Ehleringer *et al*., 1986). Ground leaf samples from each species were analyzed for $\delta^{13}C$ by the Stable Isotope Analysis Facility at the University of California, Davis. Samples were analyzed using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The final delta values are expressed relative to international standards V-PDB (Vienna PeeDee Belemnite).

Gas exchange measurements were carried out using both a LI-COR 6200 and 6400 gas exchange instruments (LI-COR Inc., Lincoln, Nebraska, USA). Three individuals of each study species were selected for measurements and replicated measurements of photosynthetic assimilation and stomatal conductance were made in mid-morning and early afternoon over several days to calculate mean maximum rates. Light response curves were measured under constant leaf-to-air vapour pressure deficit (VPD) and temperature conditions. The ambient temperature inside the leaf chamber was kept at 22°C, a level close to the maximum ambient daytime temperature when the measurements were made. The VPD was maintained

Fig. 1 A) *Lithocarpus leiophyllus*, B) *Machilus bokorensis*, C) *Syzygium antisepticum*, D) *Ardisia smaragdina*. (© M.R. Sharifi)

Table 1 Growth form, habitat, mean leaf area and ecophysiological traits of 19 common species in the heathland community of the Bokor Plateau.

Key: Growth form—Ls=Low shrub, Tr=Treelet, Sh=shrub; Habitat—Rs=Rocky soil, Ri=Riparian, Sp=Soil pockets, Co=Colonizer.

Family / species	Growth form	Habitat	Heathland height (m)	Forest height (m)	Leaf area (cm^2)	SLW ($mg\ cm^{-2}$)	SLA ($m^2\ kg^{-1}$)	$d^{13}C$ (o/oo)	Assimilation ($\mu mol\ m^{-2}\ s^{-1}$)	Conductance ($mmol\ m^{-2}\ s^{-1}$)	ci/ca
Calophyllaceae											
Calophyllum calaba var. *cuneatum*	Ls	Rs	0.8-1.5	30	25.3	14.8	67.4	-28.1	9.7	129	0.57
Clusiaceae											
Garcinia merguensis	Tr	Sp	2.0-4.0	20	13.8	14.0	71.5	-26.7	4.9	72	0.61
Ericaceae											
Rhododendron klossii	Sh	Rs	1.5-2.5	5	16.5	15.6	64.2	-30.4	6.0	74	0.55
Vaccinium bracteatum	Sh	Rs	1-1.5	6	7.0	12.1	82.3	-29.0	9.6	186	0.69
Vaccinium viscifolium	Tr	Sp	4.0	6	23.1	20.8	48.0	-29.4	6.7	105	0.63
Fagaceae											
Lithocarpus elephantum	Tr	Rs	2.0-3.0	18	115.1	17.8	56.0	-28.0	8.8	122	0.53
Lithocarpus leiophyllus	Tr	Co	1.0-4.0	5	29.2	17.7	56.6	-28.5	10.9	137	0.49
Lauraceae											
Machilus bokorensis	Tr	Rs	1.0-4.0	10	37.3	17.7	75.3	-28.9	9.7	168	0.63
Melastomataceae											
Melastoma malabarica subsp. *normale*	Ls	Co	0.5-1	3	7.3	14.2	70.1	-27.4	12.3	250	0.68
Myrtaceae											
Rhodamnia dumetorum	Ls	Co	0.5-1.5	5	6.1	19.3	51.7	ND	7.4	114	0.60
Rhodomyrtus tomentosa	Ls	Co	1.0-2.0	4	12.6	13.5	74.1	-29.4	12.1	235	0.65
Syzygium antisepticum	Ls	Rs	0.3-0.5	15	1.9	ND	ND	-27.8	11.4	222	0.65
Syzygium claviflorum	Sh	Rs	1.0-2.5	2	15.2	17.0	58.7	-27.2	8.5	167	0.66
Syzygium formosum	Tr	Ri	4.0-5.0	20	90.9	16.4	61.1	-29.5	13.4	270	0.75
Pandanaceae											
Pandanus capusi	Sh	Sp	1.5-3.5	4	ND	18.1	55.2	-26.6	3.9	53	0.58
Pentaphyllaceae											
Eurya nitida var. *nitida*	Sh	Rs	2.0-3.0	10	5.1	ND	ND	-28.1	6.4	85	0.53
Primulaceae											
Ardisia crenata subsp. *crassinervosa*	Ls	Co	1.0-1.5	3	7.7	10.0	100	-28.5	7.8	144	0.66
Ardisia smaragdina	Ls	Co	1.0-1.5	1.5	9.6	14.3	70.1	-27.9	6.4	116	0.67
Rutaceae											
Achronychia pedunculata	Tr	Rs	2.0-3.0	35	23.0	14.1	70.8	-28.0	9.6	182	0.72
Mean					**24.8**	**15.7**	**66.7**	**-28.3**	**8.7**	**149.0**	**0.62**

at 0.5–0.9 kPa. The CO_2 concentration inside the leaf chamber was kept constant at 375 mmol mol^{-1} for the light response curves with CO_2 supplied from a pressurized 12-gram gas cylinder. For the CO_2 response curves, light was provided by an internal red/blue LED light source (LI6400-02B) and kept constant at a saturating intensity of 900 μmol m^{-2} s^{-1}. Gas exchange measurements allowed a calculation of the ratio of internal CO_2 concentration within the leaf tissue to that of the ambient air. This ci/ca ratio provides a second indication of water use efficiency, with a higher ratio indicating less draw down of internal CO_2 concentration with better stomatal control and thus more efficient use of water. Although March is usually a relatively dry month at Bokor, our measurements were frequently interrupted by short but intense showers during the afternoon.

Results

Nineteen common woody species present 1.0–1.5 km north of the old hotel on the Bokor Plateau were selected for comparative study (Table 1). Seven of these were treelets with a single main stem: *Garcinia merguensis* Wight, *Vaccinium viscifolium* King & Gamble, *Lithocarpus leiophyllus* A. Camus (Fig. 1A), *Lithocarpus elephantum* (Hance) A. Camus, *Machilus bokorensis* Yahara & Tagane (Fig. 1B), and *Syzygium formosum* (Wall.) Masam. and (L.) Miq. The small stature of these treelets at the study site, typically 3–4 m in height, masks their potential to grow as tall forest trees up to 20 m or more in height in favourable sites (Table 1). This dwarfing is notable in *Achronychia pedunculata* for instance, which was only 2–3 m in height at the study site but can reach 35 m in moist forests.

Five study species had an upright shrubby form of growth: *Rhododendron klossii* Ridl., *Vaccinium bracteatum* Thunb., *Syzygium claviflorum* (Blume) Merr. & L.M> Perry, *Pandanus capusi* Mart. and *Eurya nitida* Korth. var. *nitida*. These species were typically 2–4 m in height, similar to the stature of the treelets, but had the potential to reach intermediate heights of 5–10 m in favourable sites. In addition, we sampled two low shrubs that never reached above 1.5 m in height and were often much lower. These were *Calophyllum calaba* L. var. *cuneatum* Symington ex M.R.Henderson & Wyatt-Smith which was 0.8–1.5 m in height and *Syzygium antisepticum* (Blume) Merr. & L.M.Perry (Fig. 1C), which never exceeded 0.5 m. The dwarf *Calophyllum* is especially interesting as there are varieties of this species that can reach 30 m in height.

As a comparison group to the dwarfed shrub and tree species, we included five species of low-stature colonizing shrubs 1–1.5 m in height that were common in open and disturbed areas of our study site. These were *Melastoma malabarica* subsp. *normale* (D.Don) K.Meyer, *Rhodamnia dumetorum* (DC.) Merr. & L. M. Perry, *Rhodomyrtus tomentosa* Wight, *Ardisia crenata* Sims subsp. *crassinervosa* (Walker) C.M.Hu & Vidal, and *Ardisia smaragdina* Pitard (Fig. 1D).

The study species exhibited a broad range of leaf sizes with a mean area of 24.2 cm^2, but this mean was heavily influenced by two species with large leaves. *Lithocarpus elephantum* had the largest leaves at 115 cm^2 followed by *Syzygium formosum* with leaves of 90.7 cm^2. With just one exception, treelets had leaf areas of over 20 cm^2, larger than the upright and low-growing shrub species (Table 1). All five of the low colonizing shrubs had small leaves which were less than 13 cm^2 in area, but similarly small leaf sizes were also present in several of the upright shrub species. *Syzygium antisepticum* had the smallest leaf size of 1.9 cm^2. Specific leaf weights showed a relatively small range of variation from a low of 10.0 mg cm^{-2} in *Ardisia crenata* to a high of 20.8 cm^{-2} in *Vaccinium viscifolium,* with a mean value of 15.7 cm^2 for all species (Table 1). There was no significant relationship between leaf size and specific leaf weight, or between growth form and specific leaf weight.

Mean maximum rates of leaf net assimilation ranged from a low of 3.9 μmol m^{-2} s^{-1} in *Pandanus capusi* and 4.9 μmol m^{-2} s^{-1} in *Garcinia merguensis* to a high of 13.4 μmol m^{-2} s^{-1} in *Syzygium formosum* and 12.3 μmol m^{-2} s^{-1} in *Melastoma malabarica*. The mean rate for all species was 8.7 μmol m^{-2} s^{-1} (Table 1). Values of ci/ca ratio ranged from 0.49 to 0.52, but most were close to the mean value of 0.60. There was a significant positive linear relationship between ci/ca ratio and stomatal conductance. No significant difference in photosynthetic rates or ci/ca ratio between dwarfed treelets and other growth forms was found.

Rates of stomatal conductance showed a highly significant linear relationship to rates of photosynthetic assimilation, with a mean value of 149 mmol m^{-2} s^{-1} (Fig. 2A). This relationship suggests strong stomatal control over rates of photosynthesis. Although an inverse relationship might be expected between leaf specific weight and photosynthesis, this was not present (Fig. 2B).

Values of stable carbon isotope ratio ($\delta^{13}C$) were indictive of a mesic habitat with relatively low water stress, these ranging from -30.4 o/oo in *Rhododendron klossii* to -26.7 o/oo in *Garcinia merguensis*. The mean value of $\delta^{13}C$ for all species was -28.3 o/oo. The range and mean for

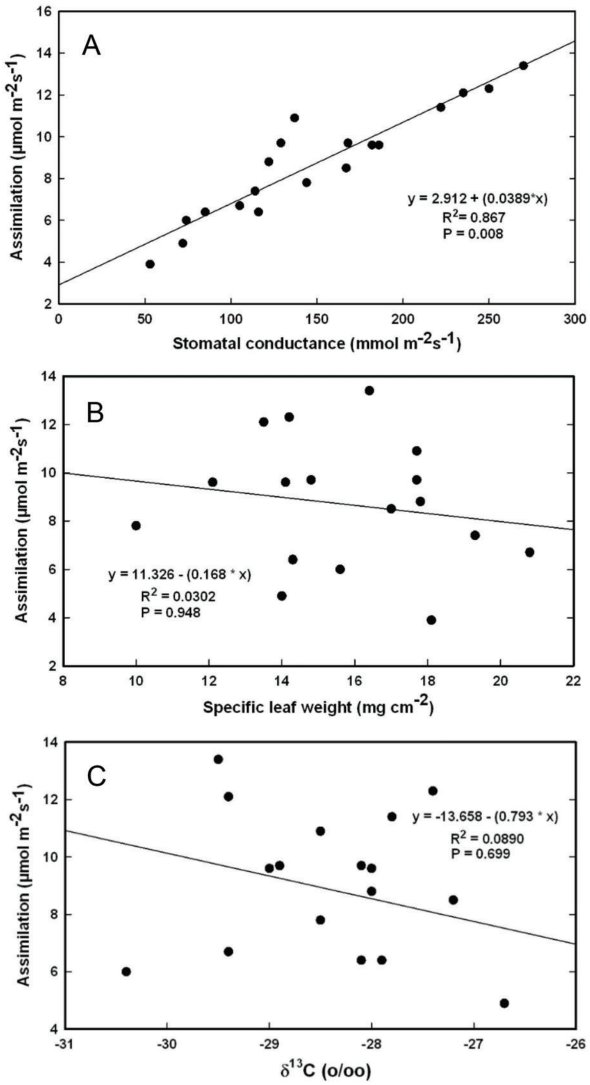

Fig. 2 Relationship of net photosynthetic assimilation to A) Stomatal conductance, B) Leaf specific weight), and C) Leaf δ^{13}C.

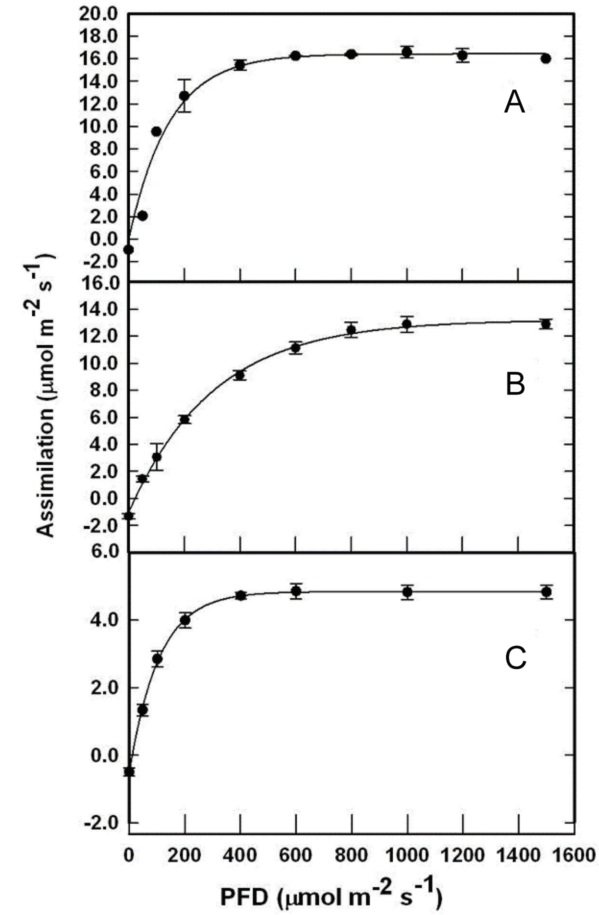

Fig. 3 Photosynthetic light respose curves: A) *Machilus bokorensis*, B) *Syzygium formosum*, and C) *Lithocarpus elephantum*.

our study species are similar to published values for wet tropical forests (Bonal *et al*., 2000). No significant relationship was present between δ^{13}C and photosynthetic rate (Fig. 2C), indicating that water use efficiency was not a strong control on photosynthesis. No significant difference in δ^{13}C between dwarfed treelets and other growth forms was found.

Light response curves measuring net photosynthetic assimilation against solar irradiance showed an adaptation to growth at relatively low light intensities which is a result of the day time cloud cover that characterizes Bokor for much of the year. *Machilus bokorensis* and *Lithocarpus elephantum* showed peak rates of photosynthesis at a light intensity of only 450-550 µmol m^{-2} s^{-1}, a level less than one quarter that of full sun, whereas *Syzygium formosum* showed higher light saturation at about 800 µmol m^{-2} s^{-1} (Fig. 3).

An unexpected result of our gas exchange studies was the observation that afternoon values of net photosynthetic assimilation were often low to very low compared to morning measurements from the same plants. In some cases, we observed complete stomatal closure during the afternoon. An example of this phenomenon is depicted with CO_2 response curves for *Lithocarpus elephantum* (Fig. 4). Despite constant temperature, VPD regulation and saturating light intensity throughout the measurements, the assimilation rate at saturating CO_2 concentrations was about 15 µmol m^{-2} s^{-1} in the morning, three times the rates observed in afternoons under identical conditions.

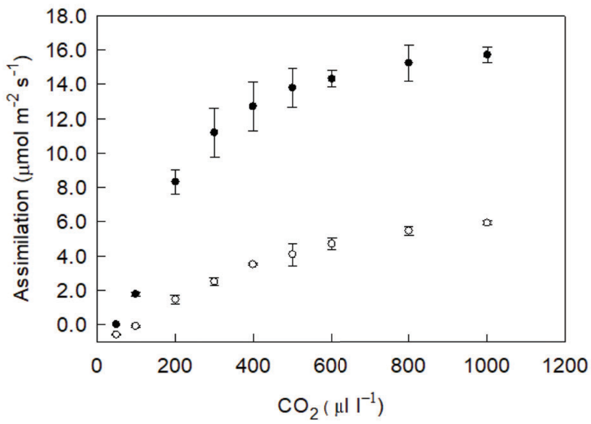

Fig. 4 CO_2 response curves for *Lithocarpus elephantum* under saturating light intensity of 900 μmol m^{-2} s^{-1} in mid-morning (closed circles) and mid-afternoon (open circles).

Discussion

The dwarfing of what are, at lower elevations, commonly tall trees involves a complex gradient in interactions between soil depth, water relations, soil nutrient availability, and wind exposure. The leaf morphological and ecophysiological traits measured in our study revealed only one trait where dwarfed treelets differed significantly from woody shrubs and low-stature colonizing shrubs. This trait was leaf size with dwarfed treelets having consistently larger leaves.

Dwarfing and restrictions on rates of tree growth could be hypothetically related to the presence of thick leaves with a high leaf specific weight in response to high winds. If this were the case, we would have expected to find the widespread presence of leaves with a high leaf specific weight. However, the ranges and means for leaf specific weight did not differ significantly between dwarfed treelets, shrubs, and low-stature colonizing shrubs in our study. Moreover, the ranges of values for our study species are consistent with published ranges for wet tropical forests (Reich *et al*., 1991; Reich, 1993; Kenzo *et al*., 2004; Long *et al*., 2015).

A variety of additional hypotheses have been proposed to explain the low stature and slow growth of tropical montane cloud forests (Weaver *et al*., 1986; Bruijnzeel & Veneklaas, 1998; Tanner *et al*., 1998; Bruijnzeel *et al*. 2011). Two of these hypotheses relate to low fertility and extreme soil acidity coupled with reduced decomposition and mineralization rates and waterlogged soils that reduce root respiration. While not tested in our research, these contributing factors are clearly present given the skeletal acidic sandstone substrate and high rainfall present on the Bokor Plateau. Strong winds are likewise responsible for impacting the architecture and stature of trees in coastal sites and are certainly a secondary factor in Bokor and many other dwarf cloud forests.

More relevant to our work is the hypothesis that cloudy conditions with low levels of solar radiation and cool growing season temperatures limit rates and total amounts of net photosynthetic assimilation (Graham *et al*., 2003). As described above, our measured rates of net photosynthetic assimilation are consistent with those reported in many other studies of wet tropical forest trees where dwarfing does not occur (Reich *et al*., 1991; Reich, 1993; Kenzo *et al*., 2004). This strongly suggests that limits on maximum rates of photosynthesis are not the cause of dwarfing and slow growth rates in heathland scrub on the Bokor Plateau. Rather than being limited by low levels of solar irradiance under frequent heavy cloud cover, our measurements demonstrate a widespread adaptation to low light conditions at Bokor with light saturation for photosynthesis at irradiance levels of only about one quarter those of full sun. This is a significantly lower light saturation level than that reported for canopy leaves of tropical Dipterocarpaceae (Kenzo *et al*., 2006). Similar photosynthetic adaptation to low light levels has previously been reported in *Dacrydium elatum* (Roxb.) Wall. ex Hook. (Podocarpaceae) in Bokor (Rundel *et al*., 2016).

Our observations of afternoon stomatal closure and low rates of assimilation are difficult to explain given what would appear to be favourable conditions in the afternoon. It has been suggested that periodic water shortages may occur in montane tropical forests where shallow rocky soils are present despite high rainfall. Although we cannot fully test this hypothesis without more controlled greenhouse and field studies (Harley *et al*., 1987), our observation of common stomatal closure in the afternoon suggests that this may be possible since stomatal closure has been observed in tropical montane cloud forests in response to high evaporative demands (Körner *et al*., 1983) and has been reported in tropical tree saplings in wet forests in Costa Rica (Oberbauer, 1985). Extreme sensitivity of stomata to soil drought has also been shown in tropical rainforest trees in French Guiana (Bonal *et al*., 2000). As such, it may be that the skeletal soils on the Bokor Plateau limit water availability on a diurnal basis due to limits on effective root volume. An alternative hypothesis was suggested by Zhang *et al*. (2009), who noted that afternoon stomatal closure in both the wet and dry season was related to high levels of photorespiration acting as a photo-protectant.

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Preliminary data on the fruit flies (Diptera: Tephritidae) of Cambodia

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មូលន័យសង្ខេប

គេមានការយល់ដឹងតិចតួចណាស់អំពីរុយផ្លែឈើ (អំបូរ Tephritidae) នៅក្នុងប្រទេសកម្ពុជា មានត្រឹមតែ ១០ប្រភេទប៉ុណ្ណោះដែលកត់ត្រាដោយHardy ឆ្នាំ១៩៧៣ និង២៧ប្រភេទ (ស្ថិតក្នុងពួក *Bactrocera*) ដោយLeblanc *et al.* ឆ្នាំ២០១៥។ ផ្អែកទៅលើសំណាកដែលប្រមូលបានបន្ថែមក្នុងខែមិថុនា ឆ្នាំ២០១៧ យើងបានធ្វើកំណត់ត្រា ៨ប្រភេទបន្ថែមទៀតសម្រាប់ប្រទេសកម្ពុជា ដែលជាកំណត់ត្រាដំបូង។ យើងក៏បានបង្កើតបញ្ជីដែលមាន ៤៤ប្រភេទរុយ ក្នុងអំបូរTephritidae) មាន១២ពួក ដែលយើងដឹងថាពួកវាមានវត្តមានក្នុងប្រទេសកម្ពុជា រួមជាមួយនិងការបរិយាយអំពីរបាយ និងជីវសាស្ត្ររបស់ពួកវា។

Abstract

The true fruit flies (Tephritidae) of Cambodia are poorly known: only 10 species were recorded by Hardy (1973) and 27 species (all of the genus *Bactrocera*) by Leblanc *et al.* (2015). Based on additional material collected in June 2017, we document eight additional species for the first time in Cambodia. We also provide a list of 44 species of tephritid flies arranged in 12 genera which are currently known to occur in Cambodia, with notes on their distribution and biology.

Keywords Cambodia, Diptera, fruit flies, Tephritidae, new records.

Introduction

In the Oriental Region, the true fruit flies (Tephritidae) include some of the most important economic pests and are represented by almost 1,000 species (Norrbom, 2004 and recent additions). Hardy (1973) listed 211 species in the Tenasserim Division of Myanmar, Thailand, Cambodia, Laos, Vietnam, Peninsular Malaysia and Singapore. This list has not been updated greatly although Hancock (1999, 2004, 2011, 2012), Hancock & Drew (1994a,b, 1999, 2004), Hancock & McGuire (2002) and Chua (2010) added some new species and records and synonymised or transferred many other species from peninsular Southeast Asia. Among these, only 10 species were previously recorded in Cambodia by Hardy (1973), based on a small collection made by N. R. Spencer at 700 m asl (above sea level) in Kirirom National Park (Kampong Speu Province) in April 1961. Additionally, 27 species belonging to the genus *Bactrocera* were collected in traps baited with cue-lure and methyl eugenol at several sites east of Kron Koh Kong in April 2011 by M. San Jose and D. Rubinoff which were documented by Leblanc *et al*. (2015).

During a visit to Cambodia in June 2017, the authors identified additional material deposited at the Cambo-

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dian Entomology Initiatives (CEI) at the Royal University of Phnom Penh and collected by the authors at the Chi Phat Community-based Ecotourism Site in Koh Kong Province (Fig. 1). The purpose of this paper is to summarize current knowledge on the fruit flies of Cambodia and hopefully stimulate further studies on the group.

Methods

In general, tephritid flies can be collected with Malaise traps, rearing of adults from fruit and other plant tissues infested by larvae, using various synthetic and organic lures in McPhail and other traps, as well as by net sweeping. During our study, flies were predominantly collected with an entomological net or aspirator, by sweeping over tree leaves, freshly cut bamboo or faeces.

All specimen material collected was deposited in the collections of I.I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine (SIZK) and CEI at the Royal University of Phnom Penh.

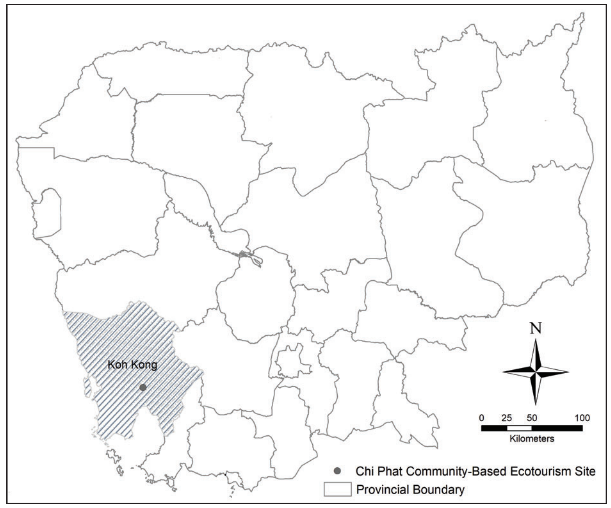

Fig. 1 Study site—Chi Phat Community-Based Ecotourism Site, Koh Kong Province.

Results

Our material comprised nine species, eight of which represent first records for Cambodia. These are documented below, together with 36 species of Tephritidae previously recorded in Cambodia.

Anoplomus Bezzi, 1913

A genus of the tribe Gastrozonini (Dacinae), which can be recognized by the combination of pointed flagellomere 1, plumose arista, 2 frontal setae, rudimentary ocellars, postocellar setae lacking, 2 pairs of scutellar setae and 2 or more long midtibial spines. Hancock (2008) included *Rhaibophleps* Hardy, 1973 and *Sinanoplomus* Zia, 1955 as synonyms. Adults of the Cambodian species were collected on Poaceae grass stems, which are possibly its host (Hardy, 1973; Hancock, 2008). Hancock (2008) provided a key to the seven species included.

***Anoplomus seclusa* (Hardy, 1973)**

Rhaibophleps seclusa Hardy, 1973: 204; Hancock, 1999: 938.

Anoplomus seclusa: Hancock, 2008: 103.

Distribution: Thailand, Laos, Cambodia (Hardy, 1973).

Bactrocera Macquart, 1835

A large genus of ca. 650 described species (Hancock & Drew, 2018b), including four recently described by LeBlanc *et al*. (2018), of predominantly Oriental and Australasian distribution. Similar to other Dacini, they are wasp-like, typically yellow-and-black flies with reduced head and body chaetotaxy (ocellar, postocellar, dorsocentral, presutural acrostichal, and katepisternal setae lacking) usually with hyaline wings except for a brown band along costal margin and a brown anal streak plus a wide cell dm. Species assigned to *Bactrocera* differ from similar species of the genus *Dacus* mainly by having abdominal tergites free rather than fused to each other, but share no obvious synapomorphies. Based on molecular phylogenetic analysis, *Bactrocera* (*sensu* Drew, 1989; White & Elson-Harris, 1992; Norrbom *et al*., 1999) has been regarded as paraphyletic (Virgilio *et al*., 2015; San Jose *et al*., 2018). As a result, species belonging to the *Zeugodacus* group of subgenera are often placed in a separate genus *Zeugodacus* Hendel, 1927 (with 191 species listed by Doorenweerd *et al*., 2018), which has a weak morphological definition and diagnosis. For this and other reasons (lack of support from morphological, biological and molecular clock data), Hancock & Drew (2018b) retained *Zeugodacus* as a subgenus of *Bactrocera*. One of us (VAK) also discussed the possible paraphyly of *Bactrocera* and insisted on keeping all the species under one subgenus until unambiguous arguments are provided. Thus, we follow the nomenclature of Hancock & Drew (2018b) here.

Bactrocera larvae usually feed on the fleshy fruit of a wide range of plant families but some infest the fruit or flowers of Cucurbitaceae. Some species including *B. dorsalis* are widespread and polyphagous pests.

For descriptions and keys, see White & Elson-Harris (1992), Drew & Hancock (1994) and Drew & Romig (2013, 2016). Nomenclature follows Hancock & Drew (2018a,b).

***Bactrocera (Bactrocera) aethriobasis* (Hardy, 1973)**

Dacus aethriobasis Hardy, 1973: 30.

Bactrocera (Bactrocera) aethriobasis: Drew & Romig, 2013: 37; Leblanc *et al*., 2015: 599.

Bactrocera aethriobasis: Doorenweerd *et al*., 2018: 25.

Distribution: Thailand (Hardy, 1973), Bhutan, Peninsular Malaysia, Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Host: *Azadirachta indica* (Meliaceae) (Drew & Romig, 2013).

***Bactrocera (Bactrocera) bhutaniae* Drew & Romig, 2013**

Drew & Romig, 2013: 51; Leblanc *et al*., 2015: 599.

Bactrocera bhutaniae: Doorenweerd *et al*., 2018: 27.

Distribution: Bhutan, India (Andaman Islands), Thailand, Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Hosts: *Xylosma brachystachys* (Flacourtiaceae) (Drew & Romig, 2013).

***Bactrocera (Bactrocera) bivittata* Lin & Wang, 2005**

Lin *et al*., 2005: 843; Drew & Romig, 2013: 56; Leblanc *et al*., 2015: 599.

Bactrocera bivittata: Doorenweerd *et al*., 2018: 27.

Distribution: China (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

***Bactrocera (Bactrocera) carambolae* Drew & Hancock, 1994**

Drew & Romig, 2013: 61; Leblanc *et al*., 2015: 599.

Bactrocera bivittata: Doorenweerd *et al*., 2018: 28.

Distribution: Thailand, Peninsular Malaysia, Singapore, Indonesia, India (Andaman Islands), Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015). Introduced to South America (Drew & Hancock, 1994).

Hosts: Wide range of fruit (Drew & Hancock, 1994; Allwood *et al*., 1999).

***Bactrocera (Bactrocera) correcta* (Bezzi, 1916)**

Drew & Romig, 2013: 69; Leblanc *et al*., 2015: 599.

Bactrocera correcta: Doorenweerd *et al*., 2018: 28.

Distribution: Pakistan, India, Nepal, Sri Lanka, Bhutan, Myanmar, Thailand, Southern China, Vietnam, Peninsular Malaysia (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Hosts: Wide range of fruit (Allwood *et al*., 1999).

***Bactrocera (Bactrocera) dongnaiae* Drew & Romig, 2013**

Drew & Romig, 2013: 75; Leblanc *et al*., 2015: 599.

Bactrocera dongnaiae: Doorenweerd *et al*., 2018: 29.

Distribution: Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

***Bactrocera (Bactrocera) dorsalis* (Hendel, 1912)**

Dacus (Strumeta) dorsalis: Hardy, 1973: 41.

Dacus (Bactrocera) dorsalis: Hardy, 1977: 49.

Bactrocera (Bactrocera) dorsalis Drew, 1989: 63 (diagnosis of complex); Drew & Hancock, 1994: 17; Norrbom *et al*., 1999: 90; Alwood *et al*., 1999: 7.

Bactrocera dorsalis: Doorenweerd *et al*., 2018: 29.

Study material: Chi Phat, 6, 8.vi.2017, 1♂, 3♀ (V. Korneyev) (SIZK).

Distribution: Nepal, Bhutan, Myanmar, Thailand, Cambodia, Laos, Vietnam, Southern China (including Hong Kong and Taiwan). Introduced in Hawaii, Marianas (USA), eradicated from Ryukyu Islands (Japan) (Drew & Hancock, 1994). Records from India, Bangladesh and Sri Lanka are now included in *B. invadens* Drew, Tsuruta & White, 2005 (Drew & Romig, 2013, 2016).

Hosts: Fruit of 40 different families (for details, see Allwood *et al*., 1999).

***Bactrocera (Bactrocera) eurycosta* Drew & Romig, 2013**

Drew & Romig, 2013: 80; Leblanc *et al*., 2015: 599.

Bactrocera eurycosta: Doorenweerd *et al*., 2018: 29.

Distribution: Peninsular and East Malaysia, Brunei, Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

***Bactrocera (Bactrocera) fuscitibia* Drew & Hancock, 1994**

Drew & Romig, 2013: 88; Leblanc *et al*., 2015: 599.

Bactrocera eurycosta: Doorenweerd *et al*., 2018: 30.

Distribution: Peninsular and East Malaysia, Indonesia, Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

***Bactrocera (Bactrocera) kanchanaburi* Drew & Hancock, 1994**

Drew & Romig, 2013: 103; Leblanc *et al*., 2015: 599.

Bactrocera kanchanaburi: Doorenweerd *et al*., 2018: 31.

Distribution: Thailand (Drew & Hancock, 1994), Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Hosts: *Artabotrys siamensis* and *Goniothalamus giganti-folius* (Annonaceae) (Allwood *et al*., 1999).

***Bactrocera (Bactrocera) kohkongiae* Leblanc, 2015**

Leblanc *et al*., 2015: 593.

Bactrocera kohkongiae: Doorenweerd *et al*., 2018: 31.

Distribution: Cambodia (Leblanc *et al*., 2015).

***Bactrocera (Bactrocera) laithieuiae* Drew & Romig, 2013**

Drew & Romig, 2013: 107; Leblanc *et al*., 2015: 599.

Bactrocera laithieuiae: Doorenweerd *et al*., 2018: 31.

Distribution: Vietnam, Thailand (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

***Bactrocera (Bactrocera) latilineola* Drew & Hancock, 1994**

Drew & Romig, 2013: 109; Leblanc *et al*., 2015: 599.

Bactrocera latilineola: Doorenweerd *et al*., 2018: 32.

Distribution: Peninsular Malaysia (Drew & Hancock, 1994), Cambodia (Leblanc *et al*., 2015).

***Bactrocera (Bactrocera) limbifera* (Bezzi, 1919)**

Drew & Romig, 2013: 110; Leblanc *et al*., 2015: 599.

Bactrocera limbifera: Doorenweerd *et al*., 2018: 32.

Distribution: India (Andaman Islands), Philippines, Indonesia, East Malaysia, Brunei, Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Hosts: *Dracontomelon dao* (Anacardiaceae), *Aglaia* sp. (Meliaceae) and *Sterculia* sp. (Sterculiaceae) (Allwood *et al*., 1999; Drew & Romig, 2013).

***Bactrocera (Bactrocera) nigrifacia* Zhang, Ji & Chen, 2011**

Bactrocera (Bactrocera) nigrifacia: Zhang *et al*., 2011: 605; Drew & Romig, 2013: 129; Leblanc *et al*., 2015: 599.

Bactrocera nigrifacia: Doorenweerd *et al*., 2018: 33.

Distribution: China (Yunnan), Thailand (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Hosts: *Callicarpa arborea* (Verbenaceae), *Capparis seblaria* (Capparidaceae), *Mellothria wallichii* (Cucurbitaceae), *Securinega virosa* (Euphorbiaceae) (Drew & Romig, 2013).

***Bactrocera (Bactrocera) nigrotibialis* (Perkins, 1938)**

Dacus (Strumeta) nigrotibialis: Hardy, 1973: 47;

Bactrocera (Bactrocera) nigrotibialis: Norrbom *et al*., 1999: 93; Drew & Romig, 2013: 129; Leblanc *et al*., 2015: 599.

Bactrocera nigrotibialis: Doorenweerd *et al*., 2018: 33.

Distribution: India, Sri Lanka, Thailand, Laos, Peninsular and East Malaysia, Brunei, Vietnam, Philippines, Indonesia (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Hosts: *Psidium guajava* and *Syzygium jambos* (Myrtaceae) (Drew & Romig, 2013). The record of *Ocimum* (Lamiaceae) is in error (D.L. Hancock pers. comm.).

***Bactrocera (Bactrocera) osbeckiae* Drew & Hancock, 1994**

Drew & Romig, 2013: 142; Leblanc *et al*., 2015: 599.

Bactrocera osbeckiae: Doorenweerd *et al*., 2018: 34.

Distribution: Thailand, Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Hosts: Flowers of *Melastoma* spp. and *Osbeckia* (Melastomataceae) (Drew & Hancock, 1994).

***Bactrocera (Bactrocera) paraarecae* Drew & Romig, 2013**

Drew & Romig, 2013: 144; Leblanc *et al*., 2015: 599.

Bactrocera paraarecae: Doorenweerd *et al*., 2018: 34.

Distribution: Bhutan (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

***Bactrocera (Bactrocera) propinqua* (Hardy & Adachi, 1954)**

Dacus (Strumeta) propinquus: Hardy, 1973: 50; 1977: 52.

Bactrocera (Bactrocera) propinqua: Drew & Hancock, 1994: 54; Norrbom *et al*., 1999: 94; Drew & Romig, 2013: 160.

Bactrocera propinqua: Doorenweerd *et al*., 2018: 35.

Distribution: Peninsular and East Malaysia, Cambodia, Singapore, Thailand, Vietnam (Drew & Romig, 2013).

Hosts: *Garcinia* spp. (Alwood *et al*., 1999), including *G. cowa* and *G. gummi-gutta* (L.) Roxb. (= *G. cambogia*). See Yong (1992) for notes on biology.

***Bactrocera (Bactrocera) thailandica* Drew & Hancock, 1994**

Drew & Romig, 2013: 182; Leblanc *et al*., 2015: 599.

Bactrocera thailandica: Doorenweerd *et al*., 2018: 37.

Distribution: Thailand, China (Yunnan), Bhutan, Brunei, Vietnam (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Hosts: *Elaeocarpus lancefolius* (Elaeocarpaceae) (Drew & Hancock, 1994).

***Bactrocera (Bactrocera) umbrosa* (Fabricius, 1805)**

Drew & Romig, 2013: 187; Leblanc *et al*., 2015: 599.

Bactrocera umbrosa: Doorenweerd *et al*., 2018: 38.

Distribution: Peninsular Malaysia and Philippines to Vanuatu and New Caledonia, Micronesia (Norrbom *et al*. 1999), Thailand, Christmas Island (Indian Ocean), Timor, (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

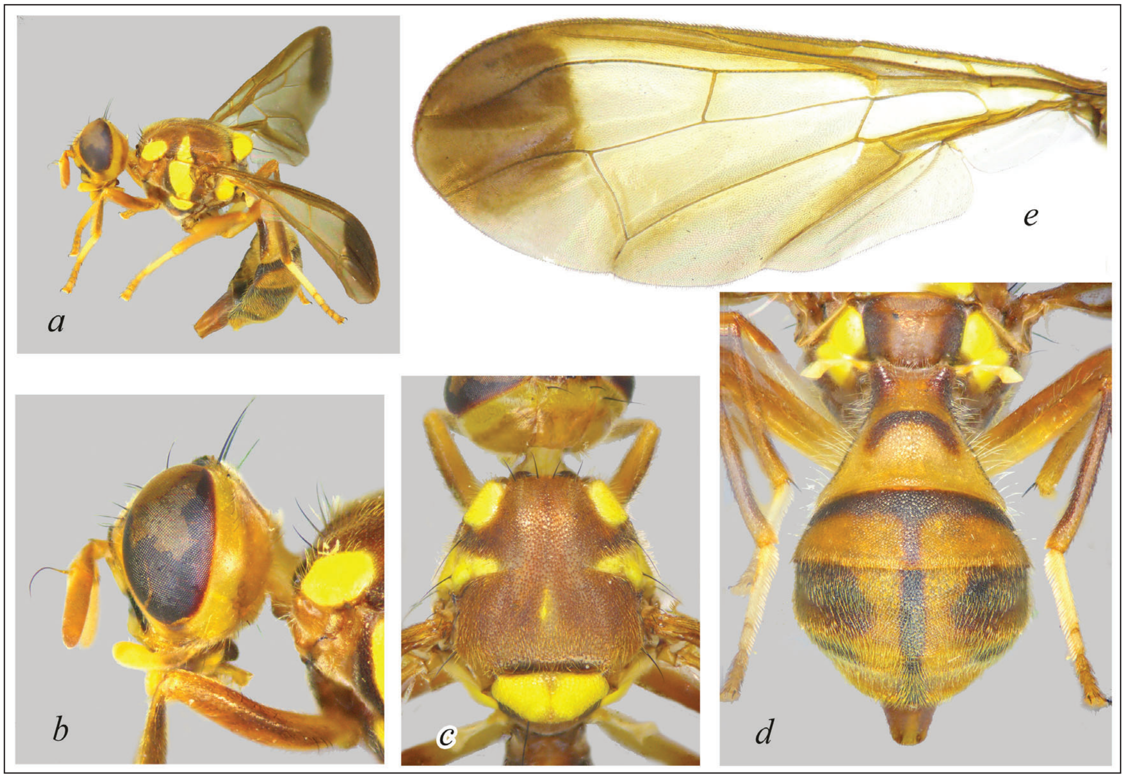

Fig. 2 *Bactrocera (Sinodacus) hochii* (Zia, 1936): A) Habitus (left), B) Head (left), C) Thorax (dorsal), D) Abdomen, E) Wing.

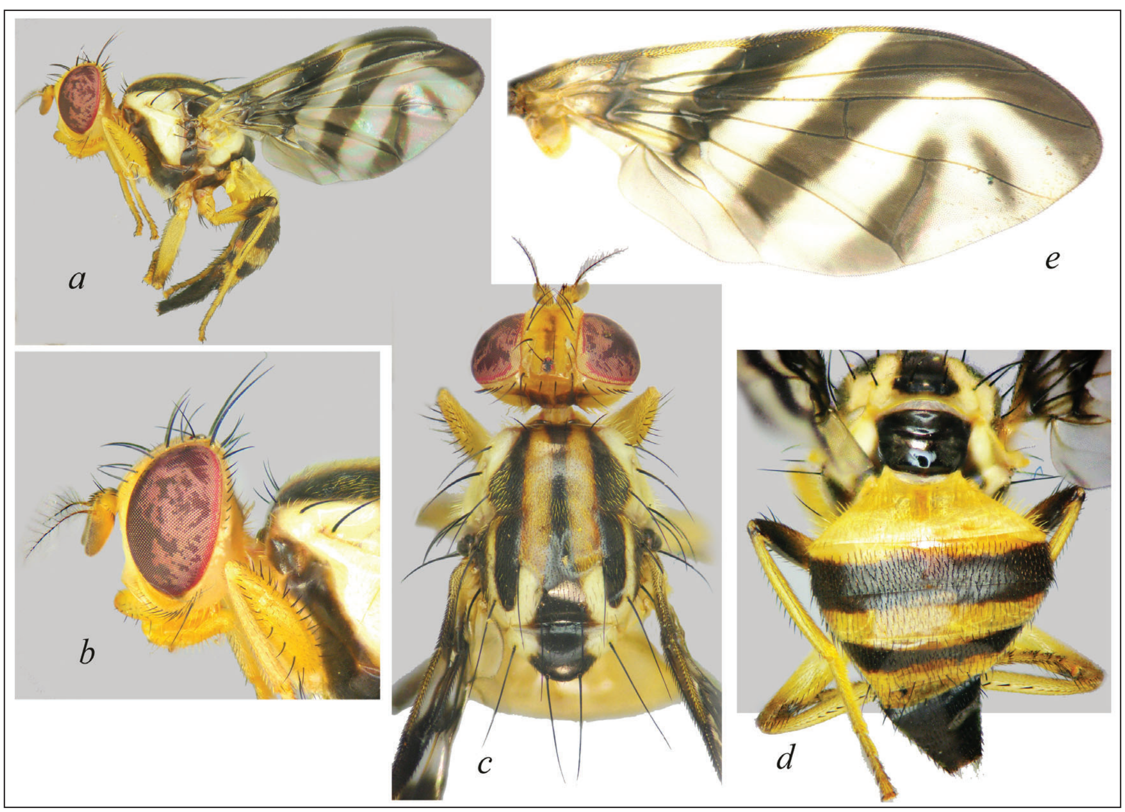

Fig. 3 *Gastrozona soror* (Schiner, 1868): A) Habitus (left), B) Head (left), C) Head and thorax (dorsal), D) Scutellum (posterior) and abdomen, E) Wing.

Hosts: *Artocarpus altilis*, *A. heterophyllus*, *A. incisa*, *A. integer* (Moraceae) (Allwood et al. 1999).

Bactrocera (Bactrocera) usitata Drew & Hancock, 1994

Drew & Romig, 2013: 187; Leblanc *et al*., 2015: 598.

Bactrocera usitata: Doorenweerd *et al*., 2018: 38.

Distribution: Peninsular and East Malaysia, Singapore, Brunei, Indonesia (Kalimantan), Thailand, Vietnam, Philippines (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Bactrocera (Javadacus) hatyaiensis Drew & Romig, 2013

Bactrocera (Zeugodacus) hatyaiensis Drew & Romig, 2013: 296; Leblanc *et al*., 2015: 599.

Bactrocera (Javadacus) hatyaiensis: Hancock & Drew, 2018b: 262.

Zeugodacus hatyaiensis: Doorenweerd *et al*., 2018: 46.

Distribution: Thailand (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Bactrocera (Javadacus) tau (Walker, 1849)

Dacus (Zeugodacus) tau: Hardy, 1973: 70.

Bactrocera (Zeugodacus) tau: White & Elson-Harris, 1992: 271; Norrbom *et al*., 1999: 104; Allwood *et al*., 1999: 22; Drew & Romig, 2013: 353.

Bactrocera (Javadacus) tau: Hancock & Drew, 2018b: 259.

Zeugodacus tau: Doorenweerd *et al*., 2018: 50.

Distribution: Cambodia (Hardy, 1973), Bhutan, Brunei, China (mainland and Taiwan), India, Indonesia (Java, Sulawesi, Sumatra), Laos, Peninsular and East Malaysia, Philippines, Sri Lanka, Thailand, Vietnam (White & Elson-Harris, 1992; Drew & Romig, 2013).

Hosts: Various Cucurbitaceae; for more detailed records see Allwood *et al*. (1999).

Bactrocera (Parasinodacus) pseudocucurbitae White, 1999

Bactrocera (Bactrocera) pseudocucurbitae White & Evenhuis, 1999: 502.

Bactrocera (Parasinodacus) pseudocucurbitae: Drew & Romig, 2013: 234; Leblanc *et al*., 2015: 599.

Bactrocera pseudocucurbitae: Doorenweerd *et al*., 2018: 35.

Distribution: Thailand, Peninsular and East Malaysia, Indonesia (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2017).

Bactrocera (Sinodacus) hochii (Zia, 1936) (Fig. 2)

Dacus (Pacifodacus) infestus Hardy, 1973: 22 (misidentification).

Bactrocera (Sinodacus) hochii: Norrbom *et al*., 1999: 100; Drew & Romig, 2013: 252; Hancock & Drew, 2018a: 191.

Zeugodacus hochii: Doorenweerd *et al*., 2018: 48.

Study material: Chi Phat, 3.vi.2017, 1♀ (V. Korneyev) (SIZK).

Distribution: Indonesia, Malaysia, Thailand, Laos, China and Vietnam (Hancock & Drew, 2018a), Cambodia (first record).

Hosts: Fruit of *Gymnopetalum cochinchinensis*, *Luffa aegyptiaca* and *Trichosanthes wawraei* (Cucurbitaceae) (Hancock & Drew, 2018a).

Bactrocera (Zeugodacus) caudata (Fabricius, 1805)

Bactrocera (Zeugodacus) caudata: Norrbom *et al*., 1999: 102; Leblanc *et al*., 2015: 599; Hancock & Drew, 2018b: 262.

Zeugodacus caudatus: Doorenweerd *et al*., 2018: 46.

Distribution: India, Sri Lanka, Myanmar, Thailand, Vietnam, China (Hainan), Taiwan, Peninsular and East Malaysia, Brunei, Indonesia (Drew & Romig, 2013), Cambodia (Leblanc *et al*., 2015).

Hosts: Male flowers of *Cucurbita moschata* (Cucurbitaceae) (Drew & Romig, 2013).

Carpomya Costa, 1854

Medium-sized (3.5–5.0 mm) fruit flies with 3 frontal and 2 orbital setae, pale postocellar seta, variable shape of head, antenna and proboscis, usually brightly patterned, pale yellow to orange mesonotum with shiny black spots and grey microtrichose areas, long and strongly acute posterior lobe of surstylus of male, oviscape with T-shaped desclerotized posteromedial area ventrally, and aculeus either uniformly tapered apically or (in the subgenus *Goniglossum*) serrated. Third instar larva with a few (3–4) serrated oral ridges and stomal sensory organ with strong preoral teeth (Korneyev *et al*., 2017). Six species in Eurasia and one in Central America. Of these, two pest species occur in the Oriental Region: *C. pardalina* Bigot, 1891 in India and *C. vesuviana*. A key was provided by Korneyev *et al*. (2017).

Carpomya vesuviana Costa, 1854

Carpomyia vesuviana: Hardy, 1973: 245.

Study material: Phnom Penh, 16.ii.2016, 1♀ (CEI).

Distribution: Palaearctic Region (Mediterranean), Oriental Region (Indian Subcontinent, Thailand) (Hardy, 1973; Norrbom *et al*., 1999), Cambodia (first record).

Hosts: Larvae in fruit of *Zizyphus jujuba*, *Z. nummularia* and *Z. sativa*.

Freyomyia Hardy, 1974

This genus belongs in the tribe Acanthonevrini of the subfamily Phytalmiinae (Korneyev, 1999). Hancock (2011) revised the concept and diagnosis of this genus and transferred the only Cambodian species here from *Rioxa* Walker. He also considered a record of "*Themara alkestis*"

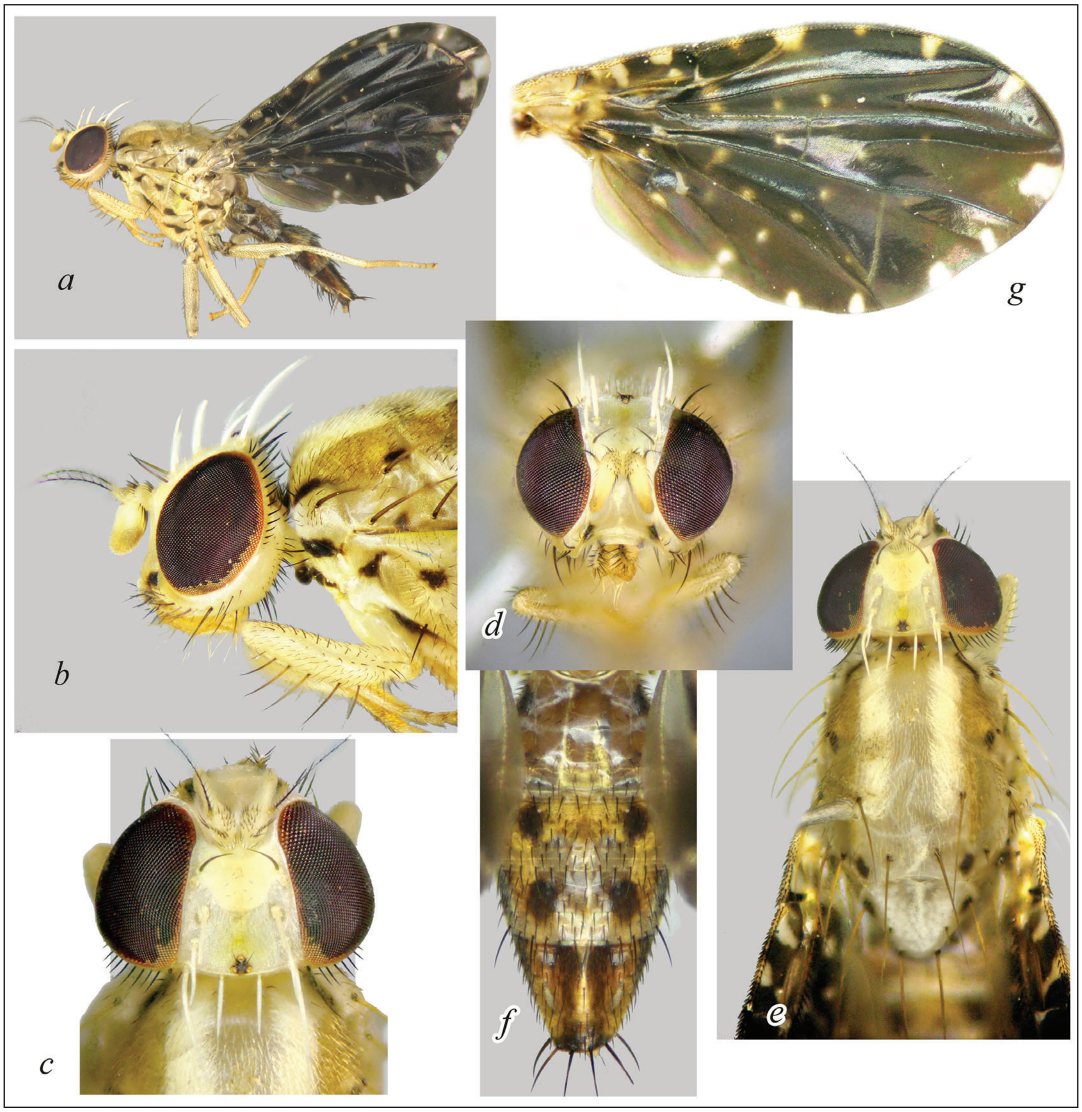

Fig. 4 *Hexacinia radiosa* (Rondani, 1868): A) Habitus (left), B) Head and thorax (left), C) Head (dorsal), D) Head and thorax (anterior), E) Scutellum (posterior, dorsal), F) Abdomen (dorsal), F) Wing.

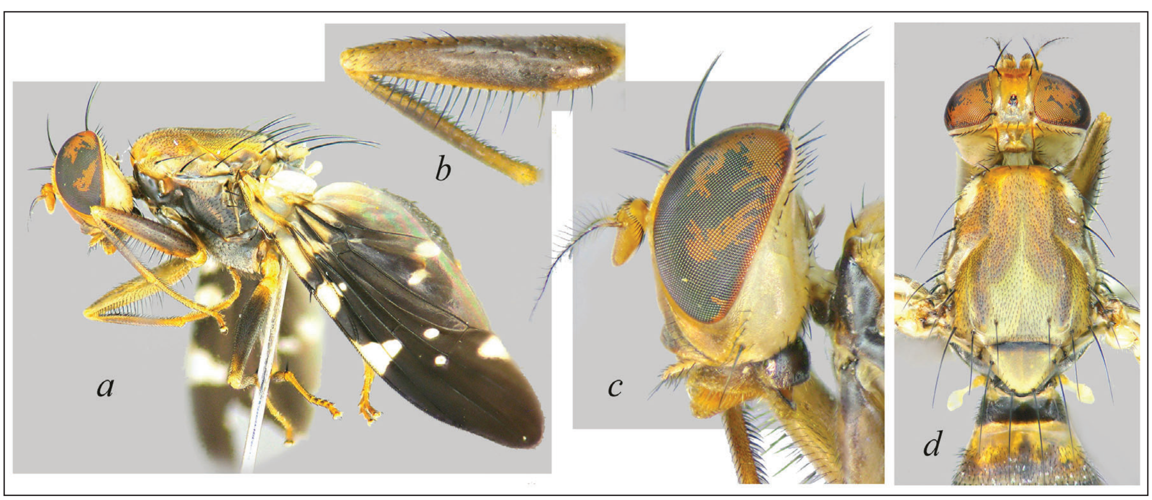

Fig. 5 *Ptilona confinis* (Walker, 1856): A) Habitus (left), B) Fore leg (posterior), C) Head (left), D) Head and thorax (dorsal).

from Kirirom National Park (Hardy, 1973) to be a misidentification of the female of this species. According to Hancock (2011: 116), wing with veins R1 and R2+3 often distinctly bowed and either with the pterostigma large, with 2 triangular hyaline indentations, or with vein R2+3 undulate and wing apex subhyaline; crossvein r-m at distal quarter of cell dm; distal hyaline indentation from costa directed towards apex of cell br and other details of wing pattern; only 2 pairs of scutellar setae (intermediate seta lacking); head rather wide, at least in males; male fore femur and tibia not densely setose ventrally.

***Freyomyia vinnula* (Hardy, 1973)**

Rioxa vinnula Hardy, 1973: 111 (♂).

Freyomyia vinnula: Hancock, 2011: 114; 117.

Themara n.sp. rel. to *alkestis*: Hardy, 1973: 112 (misidentification, ♀); Hancock, 2011: 117.

Biology: Unknown. Larvae possibly saprophagous in fallen trees or bamboo stems, similar to other Acanthonevrini.

Gastrozona Bezzi, 1913

This is the type genus of the tribe Gastrozonini (Dacinae), with nine species (Hancock & Drew, 1999; David & Hancock, 2017).

Hancock & Drew (1999) defined *Gastrozona* as having the head higher than long, with 3–5 pairs of frontal setae; third antennal segment apically rounded, arista plumose; postpronotal lobes yellow; mid tibia with 1 ventroapical thickened seta; wing with oblique brown band crossing through r-m crossvein, separated from pterostigma by a hyaline band or indentation, cell bc hyaline, band across dm-cu crossvein connected with subapical or apical brown markings; scutum black or with 2–3 black vittae, but without black spots except adjacent to scutellum; aculeus elongate, with cercal unit flattened, bearing 2 pairs of steps, long setose; 2 oblong spermathecae.

According to Dohm *et al*. (2014), some *Gastrozona* larvae feed in dead bamboo shoots lying on the ground "on the softer material of the shoot tip, where they were found in large accumulations, turning the substrate into liquid sludge." Adults are often attracted to freshly cut young bamboo shoots. Hancock & Drew (1999) and David & Hancock (2017) provided keys to species.

***Gastrozona soror* (Schiner, 1868) (Fig. 3.)**

Hardy, 1973: 195; 1988: 99; Norrbom *et al.*, 1999: 154; Hancock & Drew, 1999: 732; David & Hancock, 2017: 62.

Study material: Chi Phat, on cut young bamboo shoot, 5, 7, 8.vi.2017, 5♀ (V. Korneyev) (SIZK; CEI).

Distribution: Northeast India, Thailand, Indonesia (Java) (Hancock & Drew, 1999), Bangladesh (Khan *et al*., 2017), Cambodia (first record).

Hosts: Larvae in shoots of *Bambusa* sp. and *Dendrocalamus asper* (Allwood *et al*., 1999).

Hexacinia Hendel, 1914

Another genus of the Phytalmiinae Acanthonevrini (Korneyev, 1999). This genus can be easily recognized by the combination of very wide and dark brown, often metallic blue, disc-shaped wing (2× as long as wide) with numerous paler spots, mainly creamy white body with sparse black pattern; head with 2 pairs of frontal setae at anterior margin, the anterior seta inclinate and posterior one reclinate, often white, as orbital and vertical setae; scutellum with 3 pairs of setae; anepisternum with additional seta at the middle of ventral margin; aculeus poorly sclerotized, with separate, long setose and blunt cercal unit. Hancock (2014) discussed the genus and provided a key to the three species included. Biology is unknown, though apparently saprophagous, as are most Acanthonevrini.

***Hexacinia radiosa* (Rondani, 1868) (Fig. 4)**

Hardy, 1973: 104; 1986: 41; Norrbom *et al*., 1999: 159; Hancock, 2014: 49.

Study material: Chi Phat, attracted to faeces, 5, 8, 10, 11.vi.2017, 4♂ (V. Korneyev) (SIZK; CEI).

Distribution: India, Sri Lanka, Myanmar, Thailand, South China (Yunnan), Vietnam, Peninsular Malaysia, Philippines, Brunei, Indonesia (Sumatra) (Hardy, 1973; 1986; Hancock, 2014), Cambodia (first record).

Metasphenisca Hendel, 1914

A genus of the tribe Tephrellini (Tephritinae) with nearly 30 species in Afrotropical and Oriental Regions. Adults can be recognized by the combination of shining black thorax and abdomen, dark brown wing with 2 hyaline indentations from at anterior and 3 at posterior margin of wing, bowed costa and dark band along costal cell, short pterostigma, 3 frontal, 2 orbital, and 2 pairs of scutellar setae. Larvae feed in flowers and seeds of Acanthaceae (*Blepharis* etc.) (Hancock, 1991, 2010).

***Metasphenisca reinhardi* (Wiedemann, 1824)**

Isoconia reinhardi Hardy, 1973: 313.

Metasphenisca reinhardi: Hancock, 1991: 45; Norrbom *et al*., 1999: 159; Hancock & McGuire, 2002: 9; Hancock, 2010: 2.

Distribution: Myanmar, Thailand, Cambodia (Hardy, 1973), Sri Lanka, India, Bangladesh (Hardy, 1977). The East African record is a misidentification.

Fig. 6 *Taeniostola vittigera* Bezzi, 1913: A) Habitus (left), B) Head and thorax (left), C) Same (dorsal), D) Abdomen (dorsal), E) Wing.

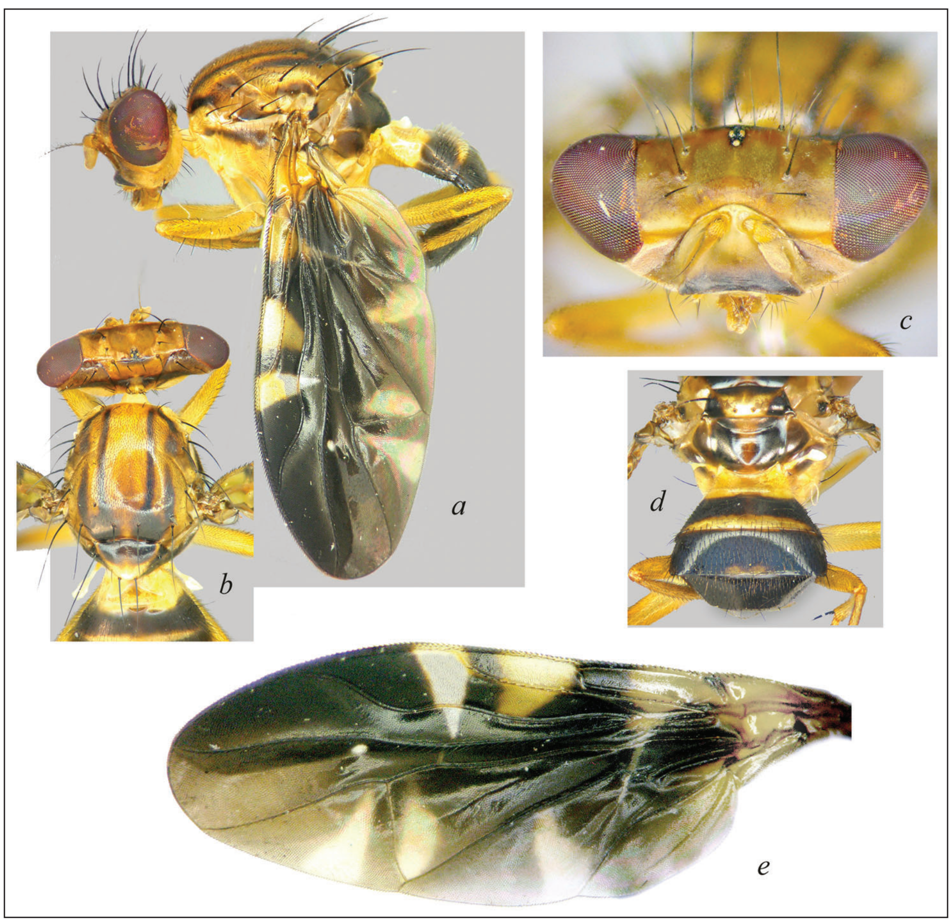

Fig. 7 *Themara yunnana* Zia, 1963: A) Habitus (left), B) Head and thorax (dorsal), C) Head (anterior), D) Scutellum (posterior) and abdomen, E) Wing.

Hosts: Unknown.

Platensina Enderlein, 1911

A genus of the tribe Dithrycini (Tephritinae) with 21 species in the Oriental and Australasian Regions (Afrotropical species assigned to this genus belong elsewhere). Adults can be recognized by the combination of subshining brown thorax and shining brown or black abdomen, dark brown, usually wide wing with numerous isolated hyaline dots, bowed costa and dark band along costal cell, short pterostigma, 3 frontal, 2 orbital, and 1–2 pairs of scutellar setae. Larvae are associated with Onagraceae (Hancock, 2012). Hancock (2012) provided a key to species.

Platensina acrostacta (Wiedemann, 1824)

Hardy, 1973: 301; 1977: 119; Hancock & McGuire, 2002: 9; Hancock, 2012: 306.

Distribution: India, Bangladesh, Sri Lanka, Myanmar, China (Yunnan), Thailand, Cambodia (Hancock, 2012).

Hosts: Larvae induce galls on *Ludwigia* (= *Jussiaea*) (Onagraceae) in India (Hardy, 1973).

Platensina intacta Hardy, 1973

Hardy, 1973: 305; 1977: 120; Hancock & McGuire, 2002: 9.

Distribution: Thailand, Cambodia, Vietnam (Hardy, 1973).

Platensina quadrula Hardy, 1973

Hardy, 1973: 307.

Distribution: India, Thailand, Cambodia, Vietnam (Hardy, 1973; Hancock, 2012).

Platensina zodiacalis (Bezzi, 1913)

Tephritis zodiacalis Bezzi, 1913: 163.

Platensina zodiacalis: Hardy, 1973: 309; 1977: 120; 1988: 49; Hancock & McGuire, 2002: 10; Hancock, 2012: 309.

Distribution: India, Sri Lanka, Nepal, Bangladesh, Myanmar, Thailand, Malaysia, Singapore, China, Laos, Cambodia, Philippines, Indonesia, Australia (Hancock, 2012).

Ptilona Wulp, 1880

This genus belongs in the tribe Acanthonevrini of the subfamily Phytalmiinae (Korneyev, 1999) with eight species occurring in the Oriental Region. According to Hancock (2011: 117), *Ptilona* can be recognized by the pleurotergite with fine, erect hairs, vein R2+3 straight, base of pterostigma with hyaline indentation usually extending to vein R4+5, only 2 pairs of scutellar setae (intermediate pair lacking), 1 or seta, and male fore femur and tibia densely setose ventrally. Larvae saprophagous, often semiaquatic in dead bamboo culms: internode cavities, under remains of sheaths, in cracks of bamboo wall, near insect holes (Dohm *et al*., 2014).

Ptilona confinis (Walker, 1856) (Fig. 5.)

Hardy, 1973: 161, 1983: 200; Norrbom *et al*., 1999: Hancock, 2011: 117.

Study material: Chi Phat, 5.vi.2017, 1♂ (V. Korneyev) (SIZK).

Distribution: Northeast India, South China (mainland and Taiwan), Philippines, Bangladesh, Burma, Thailand, Laos, Vietnam, Malaysia (Peninsular and, Sarawak), Brunei, Indonesia (Java, Kalimantan, Sulawesi and Ambon), Cambodia (first record).

Ptilona conformis Zia, 1965

Hancock, 2011: 117.

Study material: Chi Phat, 3.vi.2017, 1♂ (V. Korneyev) (SIZK).

Distribution: Southern China (Yunnan), Thailand, Laos, West Malaysia, Brunei and Cambodia (first record).

Sphaeniscus Becker, 1908

A genus of the tribe Tephrellini (Tephritinae) with eight species in the Oriental, Palaearctic and Afrotropical Regions. It can be recognized by the combination of head with 3 frontal, 2 orbital, and black postocular setae, 2 pairs of scutellar setae, entirely black mesonotum and shining black abdomen, and especially by the black-crossbanded wing. Larvae apparently in the flowers of Lamiaceae.

Sphaeniscus atilius (Walker, 1849)

Hardy, 1973: 120; 1987: 259; Hancock & McGuire, 2002: 9.

Distribution: India to eastern Russia, China, Korea, Japan (Norrbom *et al*., 1999), widespread over Oriental, Australasian and Oceanian regions (Hardy, 1987), including Cambodia (Hardy, 1973).

Taeniostola Bezzi, 1913

A genus of the tribe Gastrozonini (Dacinae), with two species (Hancock & Drew, 1999; Kovac *et al*., 2006).

Hancock & Drew (1999) defined *Taeniostola* as having head higher than long, face projecting at ventral margin, antenna with flagellomere 1 apically rounded, arista plumose; 2-3 frontal and strong ocellar setae; mid tibia with 1 strong ventroapical seta; postpronotal lobes yellow; scutum with or without black vittae but without black spots except posteriorly adjacent to scutellum, wing with brown transverse bands parallel, that through dm-cu crossvein; male without anal papillae; aculeus with cercal unit blunt, long setose; 2 oval spermathecae.

According to Dohm *et al*. (2014), *Taeniostola* adults were "reared from larvae found in felled shoots lying on the ground." Adults are attracted to freshly cut young bamboo shoots. Hancock & Drew (1999) provided a key to species.

***Taeniostola vittigera* Bezzi, 1913 (Fig. 6)**

Hancock & Drew, 1999: 761 (synonymy); Kovac *et al*., 2006: 191 (catalogue).

Taeniostola apicata: Hardy, 1973: 210; 1988: 117; Norrbom *et al*., 1999: 212.

Study material: Chi Phat, on cut young bamboo shoot, 6, 7, 9.vi.2017, 6♂, 1♀ (V. Korneyev) (SIZK; CEI).

Distribution: China (Taiwan, Yunnan), India (Assam), Myanmar, Thailand, Laos, Malaysia (Peninsular, Sarawak, Sabah), Indonesia (Borneo), Cambodia (first record).

Themara Walker, 1856

This genus belongs in the tribe Acanthonevrini of the subfamily Phytalmiinae (Korneyev, 1999) with 10 species in the Oriental Region (Hancock, 2011, 2013; Hancock & Whitmore, 2014). According to Hancock (2011: 112), *Themara* can be recognized by the pleurotergite bare, wing vein R2+3 undulate, veins M normally and Cu1, including basal portion always setulose dorsally; males usually with head broadened or eyes distinctly stalked; 3 pairs of scutellar setae (intermediate pair short but present), arista plumose, 1 frontal and 2 orbital setae, and male foreleg not densely setose ventrally. Larvae saprophagous in rotting wood (Hancock, 2013). For key, see Hancock (2011).

***Themara yunnana* Zia, 1963 (Fig. 7)**

Hancock, 2011: 115 (key, revised concept).

Study material: Chi Phat, 9.vi.2017, 1♂ (V. Korneyev) (SIZK).

Distribution: China (Yunnan), India (Hancock, 2011), Cambodia (first record).

Discussion

Research on the fruit flies of Cambodia is in its infancy and the country's fauna remains poorly known. For instance, at least 140 species are known from neighbouring Thailand (Norrbom, 2004), whereas the number of species in continental Southeast Asia exceeds 210 (Hardy, 1973). Over the course of two short collecting trips in the last 10 years, the number of species recorded in Cambodia increased from 10 to 44 as a result of collections mostly made in easily reached and unprotected areas. We estimate that Cambodia supports approximately 110–120 species of Tephritidae, and anticipate that the current species list will continue to grow as further studies are undertaken.

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Rewilding in Southeast Asia: an assessment of conservation opportunities in Western Siem Pang Wildlife Sanctuary, Cambodia

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មូលន័យសង្ខេប

អាស៊ីអាគ្នេយ៍កំពុងស្ថិតនៅក្នុងស្ថានភាពវិបត្តនៃការវិនាសផុតពូជជាសាកល ដែលនៅតាមតំបន់ការពារ និងតំបន់អភិរក្សទេសភាពជាច្រើនកំពុងតែបាត់បង់ប្រភេទសំខាន់ៗ ជាពិសេសពពួកមាំងសាសី និងតិណាសីមាឌធំៗ។ ការធ្វើឱ្យប្រសើរឡើងវិញនូវទីជម្រកគឺអាចជាវិធីសមរម្យមួយសម្រាប់ការស្តារឡើងវិញនូវប្រព័ន្ធអេកូឡូស៊ីនៅក្នុងតំបន់។ យើងបានធ្វើការវាយតម្លៃពីភាពសំខាន់នៃភាវរស់៥៦ប្រភេទដែលរងគ្រោះ (ជិតផុតពូជបំផុត ជិតផុតពូជ ងាយទទួលរងគ្រោះ) និងជិតរងគ្រោះនៃក្រុមថនិកសត្វ សត្វស្លាប និងល្មូនសម្រាប់គម្រោងធ្វើឱ្យប្រសើរឡើងវិញនូវទីជម្រក ដោយផ្តោតលើដែនជម្រកសត្វព្រៃសៀមប៉ាងខាងលិច(WSPWS) ដែលមានទំហំ១,៣២០គីឡូម៉ែត្រក្រឡា និងជាតំបន់ការពារភាគល្បសាននៃប្រទេសកម្ពុជាដែលធ្លាប់មានការរំខានខ្លាំង និងថយចុះនៃប្រភេទសំខាន់ៗជាច្រើន។ ដោយមានការលើកទឹកចិត្តក្នុងការស្តារប្រភេទឡើងវិញនៅក្នុងដែនជម្រក យើងបានធ្វើកំណត់ថ្នាក់ប្រភេទដោយផ្អែកទៅលើស្ថានភាពនៃការគំរាមកំហែងជាសាកល តួនាទីក្នុងសេវាកម្មប្រព័ន្ធអេកូឡូស៊ី ភាពសំខាន់ និងទិដ្ឋភាពជាក់ស្តែង ដូចជាឱកាសដែលអាចរកប្រភេទទាំងនោះបាននៅកម្ពុជា។ ប្រភេទដែលមានចំណាត់ថ្នាក់ខ្ពស់ជាងគេទាំង១៤ សម្រាប់ស្តារឡើងវិញរួមមានប្រភេទដែលត្រូវនាំត្រឡប់មកវិញ (ឧ.ក្រពើភ្នំ) និងប៉ូពុយឡាស្យុងដែលត្រូវធ្វើឲ្យប្រសើរឡើងវិញ (ឧ.រមាំង) និងប្រភេទដែលមានពិន្ទុលើសពី១២នៅក្នុងការវិភាគរបស់យើង (>៦៥% នៃពិន្ទុគឺសម្រាប់ប្រភេទដែលចាំបាច់ត្រូវស្តារឡើងវិញ)។ ប្រភេទដែលមានចំណាត់ថ្នាក់ខ្ពស់ភាគច្រើនគឺថនិកសត្វ។ វិធីនេះបានជួយយើងក្នុងការកំណត់ប្រភេទសម្រាប់ស្តារឡើងវិញនៅក្នុង WSPWS ទោះបីជាប្រព័ន្ធធ្វើចំណាត់ថ្នាក់របស់យើងមិនបានបញ្ចូលការកំណត់អត្តសញ្ញាណជាក់លាក់នៃការគំរាមកំហែង និងលទ្ធភាពនៃការកាត់បន្ថយទាំងនេះក៏ដោយ។ ការវាយតម្លៃនេះមានសារៈសំខាន់ខ្លាំងណាស់មុនពេលចាប់ផ្តើមគម្រោងស្តារប្រភេទឡើងវិញ ក្នុងនោះមានទាំងការនាំត្រឡប់មកវិញនៃប្រភេទ និងការធ្វើឱ្យប្រសើរឡើងវិញនូវប៉ូពុយឡាស្យុង។ សកម្មភាពកាត់បន្ថយការគំរាមកំហែង ចាំបាច់សម្រាប់ក្រពើភ្នំ និងរមាំង រួមមានពង្រឹងការអនុវត្តច្បាប់ និងការគ្រប់គ្រងតំបន់ការពារ ជាពិសេសការកាត់បន្ថយអត្រាស្លាប់ដោយការប្រើប្រាស់ឧបករណ៍នេសាទ និងអន្ទាក់ រួមជាមួយការការពារតំបន់ ជាពិសេសការធ្វើរបងការពារ។

Abstract

Southeast Asia is at the centre of the global extinction crisis with many protected areas and conservation landscapes missing key species, particularly large carnivores and herbivores. The emerging field of rewilding may be a promising conservation tool to recover ecosystems in the region. We assessed the desirability of 56 globally threatened (Critically Endangered, Endangered, or Vulnerable) and Near Threatened mammal, bird, and reptile species for rewilding

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projects focused on Western Siem Pang Wildlife Sanctuary (WSPWS), a 1,320 km^2 protected area complex in northeast Cambodia which has experienced extirpations and declines of many iconic species. Based on explicit motivations for rewilding within the sanctuary, we ranked species according to their global threat status, ecosystem service roles, charisma, and aspects of practicality such as opportunities for sourcing founders from Cambodia. The top 14 ranked candidates for rewilding included species reintroductions (e.g., Siamese crocodile *Crocodylus siamensis*) and population reinforcements (e.g., Eld's deer *Rucervus eldii*) and scored >12 points in our analyses (>65% of the score for a perfectly desirable candidate for rewilding). Most of the highly-ranked candidate species were mammals, a likely artefact of our inclusion of charisma as a criterion. This approach has helped us to identify candidate species for rewilding in WSPWS, although our ranking system did not incorporate explicit identification of threats or the feasibility of mitigating these. Such assessments are critical prior to commencing rewilding projects including reintroductions and population reinforcements. Mitigating actions required for Siamese crocodile and Eld's deer would include strengthening of protected area management and law enforcement across the landscape, particularly to reduce mortality in fishing gear and snares respectively, combined with ensuring portions of the protected area are inviolate and strictly protected, potentially through fencing.

Keywords Cambodia, conservation optimism, protected area management, reinforcement, reintroduction, restoration, rewilding, species conservation.

Introduction

Southeast Asia is at the centre of the Anthropocene extinction crisis as it supports more threatened species and is experiencing faster rates of forest loss and habitat degradation than any comparable continental area (Hughes, 2017). Weak governance, corruption, and inequality are widespread in the region and all three are strongly correlated with biodiversity loss (Amano *et al*., 2018). This is exemplified in Cambodia which experienced the fastest acceleration in deforestation rates globally between 2001 and 2014 (Petersen *et al*., 2015). Despite recent deforestation, Cambodia's protected area network remains extensively forested with large expanses of deciduous dipterocarp forest (DDF) across northern and eastern Cambodia (Wohlfart *et al*., 2014). These form the largest remnant of this threatened ecosystem globally (Tordoff *et al*., 2012). However, much of the DDF in Cambodia has suffered extensive defaunation, having experienced major declines in herbivores and carnivores over the past 75 years (Loucks *et al*., 2009; O'Kelly *et al*., 2012).

Asian elephants *Elephas maximus*, the largest land mammal in Asia, occurred widely across Cambodia as recently as the 1980s (Maltby & Bourchier, 2011). Due to extensive hunting, however, the species is now restricted in the country to just two populations exceeding 50 individuals (in the Eastern Plains and Cardamom Rainforest Landscapes) and isolated small herds elsewhere (Gray *et al*., 2014). The region's largest carnivores, tigers *Panthera tigris* and perhaps leopards *P. pardus*, are functionally extinct in Cambodia, with the last record of tigers in the country in 2007 (Gray *et al*., 2017a; Rosto-Garcia *et al*., 2018). In contrast to many temperate regions (Ripple & Beschta, 2012), the loss of top carnivores has not resulted in concurrent increases in ungulates nationally. Rather, ungulates have become scarce due to high levels of poaching, largely using wire snares for the commercial wildlife meat trade (Gray *et al*., 2017b). For example, deer populations have been depleted to such an extent that they are now extremely rare across large areas of Indochina (*sensu* Cambodia, Laos and Vietnam). Further, of the four species of wild cattle (banteng *Bos javanicus*, gaur *B. gaurus*, kouprey *B. sauveli*, and wild water buffalo *Bubulus arnee*) whose abundance in the DDF of Cambodia in the 1950s was such that the landscape was dubbed the 'Serengeti of Asia' (Wharton, 1968), kouprey are almost certainly globally extinct (kouprey), wild water buffalo are likely extirpated from Cambodia, whereas gaur and banteng have experienced substantial declines. Densities of gaur are currently too low to estimate anywhere in Cambodia, whereas banteng are effectively restricted to a single population in two protected areas in the Eastern Plains Landscape which is experiencing significant hunting-driven declines (Gray *et al*., 2016) and a relict population in Kampong Speu Province (N. Marx, pers. comm.).

Nevertheless, with extensive forested landscapes remaining across Cambodia's protected area estate (which covers ca. 40% of the country) and an apparently reform-minded Ministry of Environment, opportunities exist to recover ecosystems and populations of iconic species ('rewilding' *sensu* du Toit & Petterolli, 2019). A prime example of a landscape suitable for rewilding is Western Siem Pang Wildlife Sanctuary (WSPWS) in northeast Cambodia. A protected area complex comprising the Siem Pang and Siem Pang Khang Lech wildlife sanctuaries and approximately 1,300 km^2, WSPWS supports a matrix of DDF and semi-evergreen forest and is globally significant for conservation of characteristic birds including the largest global population of the Critically Endangered white-shouldered ibis *Pseudibis davisoni* (Wright *et al*., 2012). However, large mammals (>50 kg) are either absent, in the case of tigers and probably leopards, or occur at greatly reduced densities, in the case of banteng, gaur and Eld's deer *Rucervus eldii* (BLCP, 2012). Given the documented significance of large mammals for ecosystem functioning, particularly in savannah forests (Ripple *et al*., 2015), this defaunation raises a conservation issue above and beyond that presented by the loss of rare and culturally iconic species. It may also be impacting important habitats for significant bird populations at the site. As a consequence, development of a rewilding strategy for WSPWS has been identified as a conservation need by site managers. This study identifies possible species for rewilding efforts in WSPWS with a particular emphasis on species restoration, considers these in terms of desirability and reflects on aspects of the feasibility for recovery and rewilding in the landscape.

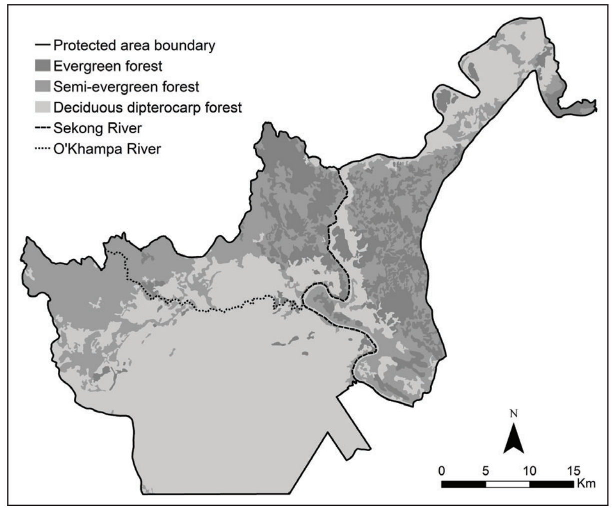

Fig. 1 Protected area boundaries, major rivers, and habitat types in Western Siem Pang Wildlife Sanctuary.

Methods

Study area

The study considered options for rewilding within the contiguous Siem Pang and Siem Pang Khang Lech wildlife sanctuaries (hereafter referred to as Western Siem Pang Wildlife Sanctuary [WSPWS] for convenience). WSPWS forms part of a network of protected areas in Laos, Cambodia and Vietnam which collectively encompass a protected land area of 11,217 km^2 (UNEP-WCMC & IUCN, 2017). WSPWS is located within the Western Siem Pang Important Bird Area (centred on 14°17'N, 106°27'E), Stung Treng Province, northern Cambodia (Fig. 1). The site is dominated by DDF, semi-evergreen forest, and riverine forest (Fig. 1), all of which occurs at low elevations (<350 m asl). The Sekong River runs approximately north to south through the site, is ca. 100–200 m wide and has a braided channel in the northern portion of the site which is dotted with small sand bars and rocky outcrops. Three smaller rivers, the O'Khampa, Stoeng Molu, and Stoeng Tin Hieng, are also present and are only partly navigable during the wet season.

WSPWS was identified as an Important Bird Area (IBA) in 2003, following the discovery of five Critically Endangered bird species at the site (Seng *et al*., 2003). Subsequent surveys have revealed nesting populations of all five Critically Endangered birds, which includes Southeast Asia's largest populations of slender-billed vulture *Gyps tenuirostris*, white-rumped vulture *G. bengalensis,* and red-headed vulture *Sarcogyps calvus*. Additionally, approximately 35% of the global population of the white-shouldered ibis *P. davisoni* and 20% of the Critically Endangered giant ibis *Thaumatibis gigantea* occur at the site (Ty *et al*., 2016; Wright *et al*., 2012). Despite a significant population of Eld's deer (ca. 50–100 individuals), the landscape supports few mammals larger than wild pigs *Sus scrofa,* with Asian elephants extirpated in Siem Pang Kang Lech Wildlife Sanctuary (recent records only exist for Siem Pang Wildlife Sanctuary) and very low numbers of banteng and gaur (Loveridge *et al*., 2018). The largest extant carnivore in the DDF landscape may now be the Asiatic golden jackal *Canis aureus,* although the mainland clouded leopard *Neofelis nebulosa* has been recorded in Siem Pang Wildlife Sanctuary (Loveridge *et al*., 2018).

Assessing rewilding feasibility

Using recent reviews of the biodiversity of WSPWS (BLCP, 2012; Loveridge *et al*., 2018), we identified all bird and mammal species considered globally threatened (i.e. Critically Endangered, Endangered, or Vulnerable) or Near Threatened by the IUCN that occur at the site or likely occurred prior to extirpation in the late 20th or early 21st century. These were considered as candidates for rewilding within the landscape and included species with no confirmed records (e.g., oriental small-clawed otter *Aonyx cinereus*) that were listed in BLCP (2012) and likely occurred historically in the landscape given their habitat preferences and known range in Southeast Asia (Table 1). Due to the lack of comprehensive data on reptiles in BLCP (2012), we independently identified eight globally threatened or Near Threatened reptile species (crocodiles and chelonians only) which had been confirmed in the site since 2005 or which were also likely to have occurred historically (Table 1).

After excluding vagrants and non-resident visitors (three bird species), we classified each candidate species as locally extant or locally extinct. Mammal species were considered locally extinct if no confirmed records were listed for WSPWS in Loveridge *et al.* (2018) and birds and reptiles were considered locally extinct if no post-2010 records existed for the landscape. For locally extinct species, it was considered that any rewilding effort would comprise reintroduction under the *IUCN Guidelines for Reintroductions and other Conservation Translocations*, and for extant species, that this would consist of population reinforcement (IUCN SSC, 2013). Following consultations with site managers, one species of ecological significance (domestic water buffalo) was included in our analysis, whereas eight globally Near Threatened bird species with known and robust populations in the landscape were omitted from analysis.

Conservation rewilding can have various motivations and the relative importance of these is dependent upon the values of the organisations and individuals involved in a rewilding effort (Moro *et al*., 2015). The main motivations for rewilding within WSPWS were to i) Restore ecological functionality to the DDF ecosystem, ii) Support conservation of globally threatened species, iii) Demonstrate the feasibility of rewilding in Asian dry forests, and iv) Promote the conservation value of the ecosystem and its biodiversity as an economic asset. Given these motivations, we assessed the suitability and 'value' of rewilding each candidate species in WSPWS by scoring these against three criteria: i) Global conservation status, ii) Ecosystem service role, and iii) Charisma. Charisma was included because of the potential role of the rewilding project to promote and showcase conservation in DDF, charismatic species being more likely to engage stakeholders, particularly government agencies (Colléony *et al*., 2017). It was also considered that charismatic species could increase the economic value of WSPWS by providing opportunities for high-end ecotourism (Hausmann *et al*., 2017). Further, because conservation translocations require sources of animals, we also scored each species according to the possibility of sourcing sufficient numbers of individuals from within Cambodia. We arbitrary decided that the three criteria would be weighted equally and higher scores represent species performing well against the motivations for rewilding (Table 2).

We assumed that rewilding species that possess a higher IUCN threat status would make a greater contribution to global species conservation. For mammals and birds, we scored species based on their published IUCN Red List status in January 2019. Critically Endangered species received a score of 4, Endangered species a score of 3, Vulnerable species a score of 2, and Near Threatened species a score of 1. Status assessments for chelonians were drawn from Rhodin *et al.* (2018) as these are updated assessments based on IUCN Red List criteria of the global conservation status of turtles and tortoises. Following relevant literature, we also assumed that large ungulate and apex carnivore species perform the most important ecosystem service roles in the DDF ecosystem (Davic, 2003; Ripple *et al*., 2014; Ripple *et al*., 2015). Consequently, we gave a score of 4 to species with a maximum body weight >100 kg or species which were apex carnivores, a score of 3 to species with a maximum body weight of 50–100 kg, a score of 2 to small to medium carnivores, frugivores and piscivores, and a score of 1 to all other species.

All conservation projects need to be practical and reintroduction or reinforcement efforts obviously require a source of appropriate animals. IUCN Species Survival Commission guidelines for conservation reintroductions recommend that founders for reintroductions 'should show characteristics (genetic, morphological, physiological, and behavioural) that are appropriate with the original populations' (IUCN SSC, 2013). While a number of studies have shown that reintroduction success is generally but not exclusively higher when wild (as opposed to captive) individuals are used (Fisher & Lindenmayer, 2000), we only considered captive populations as possible animal sources for rewilding efforts in WSPWS. This was because wild capture of sufficient individuals for rewilding efforts could impact the viability of source populations and would require considerable technical and financial resources. In the absence of clear understanding of the size of remnant populations of many of the globally threatened species assessed in our study, this was not felt to be justified. Consequently, each taxon was scored based on opportunities for sourcing individuals from appropriately managed captive populations in Cambodia. While animals could potentially be sourced from captive populations outside Cambodia, this possibility was excluded in our analysis because i) it was not possible to obtain complete data for collections held outside the country, and ii) there are substantial political, legal and practical barriers to transferring animals from neighbouring countries into Cambodia.

Table 1 Candidate species scores for rewilding in Western Siem Pang Wildlife Sanctuary (maximum score = 20). Two points were given to species which have been successfully reintroduced in Asia (Past Reintro) and two points were deducted for species associated with human wildlife conflict (HWC). The type column indicates whether a species rewilding project would be a reintroduction (ReinT), reinforcement (ReinF), or ecological replacement (EcoRe).

Species	Type	Threat	Ecosystem servicing	Sourcing	Charisma	Past Reintro	HWC	Total
Asian elephant *Elephas maximus*	ReinF	3	4	2	4		Yes	11
Gaur *Bos gaurus*	ReinF	2	4	2	2	Yes	Yes	10
Banteng *Bos javanicus*	ReinF	3	4	2	3	Yes		14
Domestic water buffalo *Bubalus bubalis*	EcoRe	0	4	4	1	Yes		11
Wild water buffalo *Bubalus arnee*	ReinT	3	4	1	4	Yes		12
Eld's deer *Rucervus eldii*	ReinF	3	3	3	3	Yes		14
Sambar *Rusa unicolor*	ReinF	2	3	3	2	Yes		12
Chinese serow *Capricornis milneedwardsii*	ReinF	1	2	3	1			7
Asiatic black bear *Ursus thibetanus*	ReinT	2	3	3	4			12
Sun bear *Helarctos malayanus*	ReinF	2	3	4	4			13
Tiger *Panthera tigris*	ReinT	3	4	1	4	Yes	Yes	12
Leopard *Panthera pardus*	ReinT	2	4	2	4	Yes	Yes	12
Dhole *Cuon alpinus*	ReinF	3	4	2	3			12
Mainland clouded leopard *Neofelis nebulosa*	ReinF	2	3	2	2			9
Fishing cat *Prionailurus viverrinus*	ReinT	2	2	2	4			10
Marbled cat *Pardofelis marmorata*	ReinT	1	2	1	3			7
Asiatic golden cat *Catopuma temminckii*	ReinF	1	2	1	1			5
Large spotted civet *Viverra megaspila*	ReinF	3	2	1	3			9
Greater hog badger *Arctonyx collaris*	ReinF	2	2	1	1			6
Hairy nosed otter *Lutra sumatrana*	ReinT	3	2	2	4			11
Smooth-coated otter *Lutrogale perspicillata*	ReinF	2	2	3	3			10
Eurasian otter *Lutra lutra*	ReinT	1	2	1	1			5
Asian small-clawed otter *Aonyx cinereus*	ReinT	2	2	2	3			9
Binturong *Arctictis binturong*	ReinT	2	2	2	3	Yes		11
Pygmy slow loris *Nycticebus pygmaeus*	ReinF	2	1	3	2			8
Annam gibbon *Nomascus annamensis*	ReinF	3	2	1	3	Yes		11
Red-shanked douc *Pygathrix nemaeus*	ReinF	3	2	1	3			9
Indochinese lutung *Trachypithecus germaini*	ReinF	3	2	3	3	Yes		13
Northern pig-tailed macaque *Macaca leonina*	ReinF	2	2	3	1		Yes	6
Black giant squirrel *Ratufa bicolor*	ReinF	1	1	2	3			7
Sunda pangolin *Manis javanica*	ReinF	4	1	3	2	Yes		12
White-winged duck *Asarcornis scutulata*	ReinF	3	2	1	2	Yes		10
Red-headed vulture *Sarcogyps calvus*	ReinF	4	3	1	3			11

Table 1 Continued.

Species	Type	Threat	Ecosystem servicing	Sourcing	Charisma	Past Reintro	HWC	Total
White-rumped vulture *Gyps bengalensis*	ReinF	4	3	1	3			11
Slender-billed vulture *Gyps tenuirostris*	ReinF	4	3	1	3			11
Indian spotted eagle *Clanga hastata*	ReinF	2	3	1	1			7
Green peafowl *Pavo muticus*	ReinF	3	1	2	3	Yes	Yes	9
Sarus crane *Antigone antigone*	ReinF	2	1	2	3	Yes		10
Giant ibis *Thaumatibis gigantea*	ReinF	4	2	3	4			13
White-shouldered ibis *Pseudibis davisoni*	ReinF	4	2	3	3			12
Asian woolly-neck *Ciconia episcopus*	ReinF	2	1	4	2			9
Greater adjutant *Leptoptilos dubius*	ReinF	3	2	2	3			10
Lesser adjutant *Leptoptilos javanicus*	ReinF	2	1	4	2			9
Great slaty woodpecker *Mulleripicus pulverulentus*	ReinF	2	1	1	2			6
Siamese crocodile *Crocodylus siamensis*	ReinT	4	4	4	3	Yes	Yes	15
Elongated tortoise *Indotestudo elongata*	ReinF	4	1	4	1			10
Asian giant softshell turtle *Pelochelys cantorii*	ReinF	4	1	3	2			10
Yellow-headed temple turtle *Heosemys annandalii*	ReinT	4	1	3	1			9
Southeast Asian box turtle *Cuora amboinensis*	ReinF	3	1	4	1			9
Giant Asian pond turtle *Heosemys grandis*	ReinF	3	1	2	2			8
Southeast Asian softshell turtle *Amyda ornata*	ReinT	2	1	3	1			7
Mekong snail-eating turtle *Malayemys subtrijuga*	ReinF	1	1	1	1			4

Table 2 Summary of criteria used for assessing species desirability for rewilding in Western Siem Pang Wildlife Sanctuary.

Criteria	Score			
	4	3	2	1
IUCN Threat Status	Critically Endangered	Endangered	Vulnerable	Near Threatened
Ecosystem Servicing	>100 kg / top carnivores	50-100 kg	Carnivores, frugivores, piscivores	Other
Sourcing (individuals in managed conservation breeding facilities in Cambodia)	>50	11–49	1–10	0
Charisma (ranking in MacDonald *et al*., 2017)	1–50	51–150	151–500	>501
Other	0.3 (±0.2)	5.8 (±1.8)	0.9 (±0.3)	2 (±0.4)

Appropriately managed captive populations of globally threatened and Near Threatened species exist at two facilities in Cambodia: the Phnom Tamao Wildlife Rescue Centre (PTWRC) and the Angkor Centre for Conservation of Biodiversity (ACCB). The PTWRC is located outside Phnom Penh and is managed by the Cambodian government with technical and financial support from international conservation organisations, primarily Wildlife Alliance. The vast majority of animals in PTWRC originate from the illegal wildlife trade and the facility has been used to source individuals for ongoing reintroduction efforts including reintroduction of pileated gibbons *Hylobates pileatus* into forests surrounding the Angkor Wat temples (Le Roux *et al*., 2019). The ACCB is located outside Siem Reap and is managed by Münster Zoo (Allwetterzoo). It principally hosts collections of large waterbirds and reptiles. The goals of the ACCB include species conservation and population restoration with an emphasis on *ex situ* breeding efforts for threatened species.

We obtained the number of each candidate species in the collections of PTWRC and ACCB. Species with >50 individuals in PTWRC or with ongoing *ex situ* breeding efforts at ACCB were given a score of 4, whereas species with between 11–49 individuals in PTWRC and ACCB were given a score of 3. Species with 1–10 individuals in PTWRC and ACCB were given a score of 2, whereas all other species were given a score of 1. As there were no pragmatic options for sourcing individuals of kouprey, Javan rhinoceros *Rhinoceros sondaicus*, amd Sumatran rhinoceros *Dicerorhinus sumatrensis*, these were given a score of 0.

We scored the charisma of each candidate mammal species using MacDonald *et al*. (2017) who modelled the appeal of all terrestrial mammals (4,320 species) based on interview surveys conducted globally. Candidate species included in the top 50 most appealing species were given a score of 4, whereas those ranked between 51–150 were given a score of 3. Candidates ranked between 151–500 were given a score of 2, whereas the remainder received a score of 1. In the absence of similar models for birds and reptiles, the lead author allocated each species a charisma score based on his personal judgement (Table 1).

Two additional factors that may influence the ease and desirability of a rewilding project were also considered: practicality and risk. On practicality, two additional points were given to a species if we were able to find information confirming that reintroduction or population reinforcement efforts had been undertaken in Asia which resulted in the breeding of translocated individuals in the wild. We acknowledge that while this does not necessarily indicate successful reintroduction, it does at least demonstrate that such a project is practically and technically feasible. On risk, two points were deducted from the score for a species if it was deemed through literature review and our field experience to pose a risk to human populations or livelihoods as a result of human wildlife conflict.

Results

We assessed a total of 56 taxa (34 mammals, 14 birds, and eight reptile species) for rewilding desirability in WSPWS (Table 1, Fig. 2). These species represented 21 reintroductions, 34 population reinforcements, and one ecological replacement (domestic water buffalo). Thirteen species assessed (five birds, four reptiles and four mammals) were listed by the IUCN as Critically Endangered and 15 were listed as Endangered (11 mammals, two birds and two reptiles).

Twelve species received the highest score for ecosystem service functioning: four apex predators (Siamese crocodile *Crocodylus siamensis*, leopard, tiger, and dhole *Cuon alpinus*), and eight herbivores weighing >100kg (Asian elephant, four wild cattle species, domestic water buffalo, and two rhinoceros species). Eight of our candidate species were modelled by MacDonald *et al*. (2017) as among the top 50 most charismatic mammals on the planet: Asian elephant (ranked 1st), wild water buffalo (2nd), tiger (6th), sun bear *Helarctos malayanus* (13th), Asiatic black bear *Ursus thibetanus* (12th), leopard (17th), hairy-nosed otter *Lutra sumatrana* (34th), and fishing cat *Prionailurus viverrinus* (39th). We also gave the highest score to giant ibis, this being the national bird of Cambodia, and an icon for ecotourism and community outreach activities in the country. Seven species received the highest score for ease of sourcing within Cambodia. These were Siamese crocodile and sun bear, with more than 50 individuals at PTWRC, and Asian woolly-neck *Ciconia episcopus*, lesser adjutant *Leptoptilos javanicus*, elongated tortoise *Indotestudo elongata*, and Southeast Asian box turtle *Cuora amboinensis*, due to established captive breeding efforts at ACCB. The ubiquitous domestic water buffalo was also given a score of four points. Finally, we found evidence that 17 of our taxa had been subject to ongoing 'successful' reintroduction or translocation projects in Asia, whereas seven taxa had points deducted for potentially being a cause of human wildlife conflict (Table 1).

None of our candidate species scored the theoretical maximum of 20 points. Indeed, only 14 species scored >12 points, equivalent to >65% of the score for a perfectly desirable candidate for rewilding (Fig. 3). The highest rated taxon, with 15 points or 75%, was the Siamese

Fig. 2 Selected candidate species for rewildling in Western Siem Pang Wildlife Sanctuary. Clockwise from top-left: elongated tortoise *Indotestudo elongata*, Eld's deer *Rucervus eldii* (© J.C. Eames), Siamese crocodile *Crocodylus siamensis* (© J. Holden / Wildlife Alliance), and white-winged duck *Asarcornis scutulata* (© J.C. Eames).

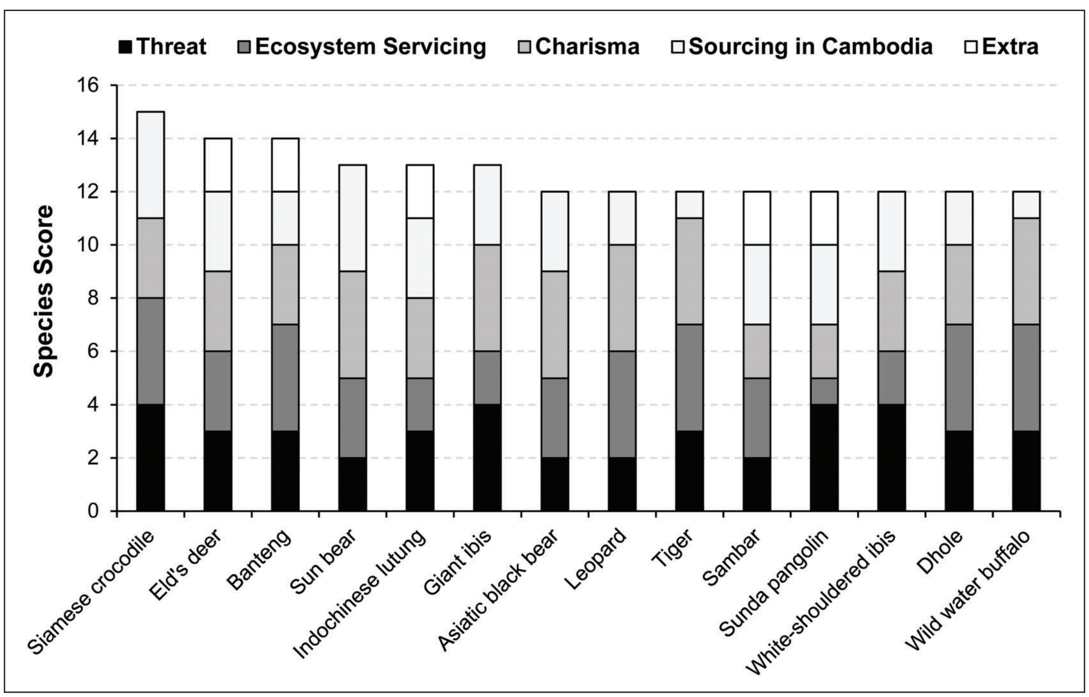

Fig. 3 Highest-ranked species for rewilding in Western Siem Pang Wildlife Sanctuary based on the sum score for four equally-weighted criteria. Extra points were given to species which have been successfully reintroduced in Asia in the past.

crocodile. This was closely followed by banteng and Eld's deer, both of which scored 14 points. The highest-ranking birds were giant and white-shouldered ibis with 13 and 12 points, respectively. The species that were ranked lowest and so the least desirable for rewilding based on our approach were the Mekong snail-eating turtle *Malayemys subtrijuga* with four points, followed by Asiatic golden cat *Catopuma temminckii* and Eurasian otter *Lutra lutra* with five points.

Discussion

We formulated a framework for identifying suitable species for rewilding projects (once appropriate feasibility studies are completed) and applied this to WSPWS, a globally significant area for conservation in northeast Cambodia. Uncritical application of the term 'rewilding' to conservation restoration projects has recently been criticized (Hayward *et al*., 2019) and du Toit & Pettorelli (2019) attempted to define the key aspects of rewilding. Based on these principles, our conservation vision for WSPWS has characteristics of both restoration and rewilding (du Toit & Pettorelli, 2019). However, we prefer to use the term rewilding because we believe this demonstrates the novelty of our approach within an Indochinese context where there is limited history of restoration. Pragmatically, use of the term rewilding also has considerable additional value for promotion and fund-raising.

We assessed the 'desirability' of rewilding 56 taxa listed as globally threatened or Near Threatened in the *IUCN Red List*. These species would constitute 21 reintroductions (i.e. species known to be extirpated from WSPWS), 34 population reinforcements (i.e. species with extant populations in WSPWS), and one ecological replacement (domestic water buffalo). However, because the current status of a number of taxa (e.g., marbled cat *Pardofelis marmorata*) is unknown in WSPWS, it is unclear whether a rewilding project would constitute a reintroduction or a reinforcement. The criteria we used for assessing desirability for rewilding and their relative weighting were influenced by the site-specific goals of the managers of WSPWS and as such, our scoring system is largely subjective in the sense that it is site-specific and driven by local experts. Despite these caveats, we feel that our results identify species which should be seriously considered for rewilding the landscape and for which thriving populations in WSPWS would provide important ecosystem services. They would also be of high global conservation value and constitute flagships for rewilding in tropical Asia and conservation of dry and semi-evergreen forests in Cambodia.

However, robust feasibility and risk assessments need to be conducted prior to any rewilding actions for all of the species considered. This is particularly true given that we deliberately did not address one of the most critical aspects of any conservation translocation: threat mitigation. IUCN guidelines state that reintroductions and population reinforcements are not advised if threats have not been mitigated (IUCN SSC, 2013). Thus, any feasibility plan for rewilding in WSPWS would need to explicitly identify threats to the target taxa and state measures required to mitigate or avoid impacts on reintroduced or supplemented populations. Evidence that threats identified were sufficiently reduced would also be needed prior to any animal releases. Only then could any of the species we assessed as desirable for rewilding be considered suitable. Currently, threats to most of the species we analysed in WSPWS are extensive and increasing due to a combination of insufficient law enforcement, infrastructure development, and growing human populations. Effective threat mitigation would therefore likely be the most difficult and expensive aspect of any rewilding effort in WSPWS. In the following sections, we discuss several of the top-ranked species in from our analysis and identify some of the threats and mitigation efforts which would need to be undertaken prior to any rewilding effort.

The Siamese crocodile was jointly ranked as the most desirable species for rewilding in WSPWS. The species is Critically Endangered with an estimated population of <400 wild individuals remaining across 35 localities in Cambodia (Bezuijen *et al*., 2012). More than 75% of the occupied waterways and 90% of the population are in the Cardamom Rainforest Landscape, southwest Cambodia (Han *et al*., 2015). Given its global conservation status, establishment of a new population in northeast Cambodia, where the species was likely extirpated in the early 2000s, would be of clear conservation value. Population reinforcement efforts for Siamese crocodile are ongoing in Cambodia using individuals from captive populations at the PTWRC and crocodiles head-started from harvested wild nests. Between 2011 and 2017, 81 such crocodiles were released into the Cardamom Mountains (Eam *et al*., 2017; J. Frechette, pers. comm.). The apparent success of these efforts and availability of individuals for rewilding in WSPWS were factors that contributed to the high score of the species in our assessment.

While hunting for skins and capture to stock legal commercial crocodile farms were major drivers of the historic decline of Siamese crocodile, the greatest threats to populations in Cambodia are now habitat loss and degradation and incidental capture and drowning in fishing gear (Bezuijen *et al*., 2012). Due to the habitat loss and hydrological changes caused by hydropower development, this has also been identified as a threat across Southeast Asia (Bezuijen *et al*., 2012). Reintroduction of Siamese crocodile to WSPWS would require identification of stretches of largely undisturbed and near-pristine riverine habitat and active law enforcement to reduce human disturbance and illegal fishing in such sites. The existence of and potential for future hydropower developments within the Sekong River would also need assessment. Siamese crocodiles are widely believed to pose minimal threat to humans and communities that have co-existed with the species for generations continue washing, bathing and swimming in the same waterbodies with little hesitation (Han *et al*., 2015). However, Cambodians living in areas where crocodiles have been absent for several decades or more tend to be fearful of them (Han *et al*., 2015). As most residents in WSPWS would have never observed crocodiles, the social implications of returning a large and 'ferocious' carnivore to the landscape would need to considered and mitigated. While local informants have reported that Siamese crocodile still occurs in WSPWS (present authors, pers. obs.), we believe this reflects an example of collective memory rather than the current situation. In the only village in WSPWS (Kampourk), a Buddhist temple flies a flag depicting a crocodile (present authors, pers. obs.). This could present an intriguing opportunity to engage local religious leaders to promote community support for reintroduction of the species.

Our analysis identified Eld's deer and banteng among the most desirable species for a rewilding project comprising population reinforcement in WSPWS. Eld's deer is endemic to the dry forests of Southeast Asia and surrounds and wild populations of the *siamensis* subspecies are now restricted to the DDF in northern and eastern Cambodia and two sites in Laos (Gray *et al*., 2015). These populations are small (likely considerably fewer than 100 individuals), fragmented, and suffer from high levels of anthropogenic mortality (primarily hunting and killing by domestic dogs). WSPWS may support one of the largest remaining populations of the *siamensis* subspecies globally, with a minimum estimate of 39 adults in April 2018 (Eames, 2018a). Historically, the species would have been abundant throughout the dry forests and as presumably the most naturally abundant deer would have provided significant ecosystem services through herbivory, wallowing (by males during the rut), trampling, and as prey for large carnivores. Managed populations of Eld's deer in Hainan exceed 50 individuals per km^2, densities which seem likely to be close to the natural carrying capacity of forests in Cambodia, and which are similar to the densities of functional equivalents in similar South Asian habitats (Jathanna *et al*., 2003; Zeng *et al*., 2005; Gray *et al*., 2015). Given the global conservation status of the species, the significance of the population in WSPWS, and its potential ecosystem service role, Eld's deer would clearly be a good candidate for rewilding in WSPWS provided the impact of hunting can be mitigated.

Twenty-four Eld's deer (presumably *siamensis*) are currently in captivity at PTWRC. However, as this population originated from only two individuals and has not been subjected to conservation management, it is potentially vulnerable to inbreeding depression. There are also ca. 75 individuals of the *siamensis* subspecies in captivity in Thailand. However, it may be difficult to source these for rewilding efforts in Cambodia due to political and/or institutional constraints (N. Marx, pers. comm.). Thai conservationists have already reintroduced the *thamin* subspecies in western Thailand (Bhumpakphan *et al*., 2003). Capture of wild individuals from relict and declining populations in Cambodia such as the one at Ang Trapeang Thmor in Banteay Meanchey Province would be logistically difficult, expensive and politically challenging. Prior to initiating a rewilding project for Eld's deer in WSPWS, we recommend an assessment of sourcing options and viability of the population in WSPWS to determine the conservation value, in terms of reducing extinction probability and increasing the population, of supplementation using a range of realistic numbers. The most significant threats to Eld's deer in WSPWS are predation of fawns by domestic dogs, hunting for meat and trophy antlers with guns, and mortality in snares set for all ungulates (Gray *et al*., 2015). A clear strategy for dealing with these threats would need implementation prior to any translocation. This would need to ensure significantly improved levels of law enforcement patrolling and protected area management, potentially within a fenced portion of WSPWS, together with a programme for community education and domestic dog control, which would ultimately include lethal control.

Banteng scored as highly as Eld's deer, being a globally Endangered large ungulate with presumably significant ecosystem service roles which has been successfully reintroduced into national parks in Thailand (Chaiyarat *et al*., 2017). Though banteng require a mixture of open deciduous dipterocarp and more evergreen forest types (Gray, 2012), the species is characteristic of the dry forests of the Lower Mekong and faces threats similar to Eld's deer (Gardner *et al*., 2016). However, numbers of banteng in WSPWS are extremely low with only a small number of camera-trap photographs (one male, one female, and one calf) from April 2013 reported by Loveridge *et al*. (2018), possibly the last banteng in the landscape. Sourcing banteng would also be more problematic than Eld's deer with currently only two bulls held at PTWRC. While translocation of wild animals was not considered in this study, a recently-identified banteng population numbering 30–50 animals in a 1,000 ha forest enclave in Kampong Speu Province could be considered for translocation if conventional conservation measures *in situ* fail (N. Marx, pers. comm). The threat mitigation needs in WSPWS would be similar to those for Eld's deer and it may be possible to source banteng from Thailand where expertise in their translocation also exists.

Other candidate species which scored 12 or more points included the two bear species, one primate (Indochinese lutung *Trachypithecus germaini*), three top-carnivores (leopard, tiger, and dhole), two ungulates (sambar *Rusa unicolor* and wild water buffalo), Sunda pangolin *Manis javanica* and the two Critically Endangered ibises (giant and white-shouldered ibis). There are significant captive populations of sun bears (80) and Asiatic black bears (38) at the Free the Bears facility in PTWRC that originate from confiscations from the wildlife trade. Wildlife Alliance has reintroduced rehabilitated sun bears in the southern Cardamom Rainforest Landscape and therefore has the institutional expertise to undertake such a project. However, adequate mitigation of snaring to prevent re-capture of released animals remains an obstacle to success. For example, the initial release of two radio-collared bears Cardamom Rainforest Landscape was aborted after both individuals were caught in snares. Rehabilitated in captivity, one was subsequently released and lived for almost a year before being predated by another wild sun bear (N. Marx, pers. comm.).

Twenty-five Indochinese lutungs are currently held in PTWRC but these likely represent the nominate form. *Trachypithecus germaini margarita*, which is increasingly regarded as a separate species, is the form likely to occur in WSPWS (Moody *et al*., 2011). Habitat monitoring at WSPWS also reveals that riverine forest, the habitat apparently preferred by the species, is the most threatened forest type in the landscape due to preferential clearance for agriculture (BirdLife Cambodia, unpublished data). The Critically Endangered Sunda pangolin is notoriously difficult to breed in captivity, but live individuals are often confiscated from the illegal wildlife trade and Wildlife Alliance have released radio-tagged individuals into the Cardamom Rainforest Landscape (N. Marx, pers. comm.). In July 2019, a Sunda pangolin confiscated at WSPWS was released in the wildlife sanctuary (present authors, pers. obs.).

As Asia's most recognizable and charismatic mammal and the top carnivore across its historical range, tiger was not surprisingly identified as desirable for rewilding in WSPWS. Indeed, there are active, albeit potentially controversial, plans to reintroduce tigers to Cambodia, with the dry forests of the Eastern Plains Landscape and the rainforests of the Cardamom Mountains identified as prime reintroduction sites (Gray *et al*., 2017d). Given the ecological similarity of WSPWS to the Eastern Plains Landscape, there is no fundamental reason why the 11,217 km^2 protected area complex which it forms part of would not also be suitable for tiger reintroduction. However, constraints identified by Gray *et al*. (2017d) and Miquelle *et al*. (2018) would apply, including insufficient ungulate prey, poor law enforcement and protected area management and limited community support and engagement. In contrast to Siamese crocodiles, well-documented cases of livestock and human fatalities caused by tigers exist across their global range (Inskip *et al*., 2013). The lack of an unambiguously acceptable source for tigers also reduces their feasibility for reintroduction in WSPWS. The high ranking of tiger in our assessment highlights both the strength and weaknesses of our approach. The species is being considered for transformational rewilding projects in Cambodia, but the barriers to success, most notably threat mitigation, are substantial.

Sourcing wild water buffalo would be close to impossible, but domestic water buffalo represents an ecological analogue which also scored highly (11 points). Historically, wild water buffalo played an important role in maintaining habitat diversity, particularly around waterholes, in DDF throughout Southeast Asia (Wharton, 1968). Following extensive declines in numbers of wild ungulates and Asian elephants, the wallowing and grazing of domestic water buffalo *Bubalus bubalis* played a similar role in maintaining the ecological integrity of forest pools (Wright *et al*., 2013). However, buffalo ownership in many DDF areas is decreasing due to agricultural modernisation. In WSPWS for example, 80% of buffalo herd owners have reported a desire to replace their buffaloes with hand-tractors within the next few years (BirdLife Cambodia, unpublished data). Wright *et al*. (2013) hypothesised that a future absence of domestic water buffalo from the site would increase sedimentation and vegetation at waterholes and thereby reduce their suitability for white-shouldered ibis. This is because domestic water buffalo live almost as feral animals in WSPWS, being rounded up only once per year (present authors, pers. obs.). However, recent experiments in WSPWS failed to find convincing evidence that small herds of domestic water buffalo significantly impact waterhole structure (Eames *et al*., 2018b). Nevertheless, the release of forest-adapted and drought-resistant domestic water buffaloes into WSPWS would likely have important ecological benefits and help to replicate historic grazing and wallowing patterns within the dry forest. This approach would be similar to many of the trophic rewilding projects being initiated in Eurasia (Pereira & Navarro, 2015), with the added benefit of providing additional biomass for the Critically Endangered vulture population at the site. As gun-hunting for trophy horns is likely to have caused the extirpation of wild water buffalo from Cambodia (present authors, pers. obs.), any rewilding of domestic water buffalo would need to be coupled with improved law enforcement patrols on the ground. Indeed, since the construction of a border road along the northern border of WSPWS which separates Laos and Cambodia, poaching of domestic water buffalo by Lao hunters has increased (present authors, pers. obs.).

The highest-ranked bird species, largely as a result of their Critically Endangered status and high charisma scores, were the giant and white-shouldered ibises, both of which breed in WSPWS. The ACCB is currently establishing insurance *ex situ* captive populations of both. However, threats to the ibises are poorly understood and until these are clarified and evidence shows that they have been mitigated, we do not recommend them for rewilding and believe that the focus should remain on establishing viable *ex situ* populations. The white-winged duck *Asarcornis scutulata* has been released in protected areas in Thailand, including Huai Kha Khaeng Wildlife Sanctuary (authors, pers. obs.) and is therefore a potential candidate for reintroduction. Many of the mitigating actions required for reintroducing Siamese crocodiles (see above) would also benefit this species. However, the flightless period during moulting renders these ducks particularly susceptible to hunting. A lack of sourcing options (no captive individuals exist in Cambodia) and limited information on the ecosystem service roles of the species resulted in it receiving a score of 10. Hornbills (Bucerotidae) play an important ecosystem service role in Asian forests through seed dispersal (Corlett, 2017) and the oriental pied hornbill *Anthracoceros albirostris* has been successfully reintroduced to Singapore (Cremades *et al*., 2011). Two possible hornbills for rewilding in WSPWS, great hornbill *Buceros bicornis* and wreathed hornbill *Rhyticeros undulatus*, both of which are now considered globally Vulnerable, scored 10 and 9 points respectively. These have been released in the Cardamom Rainforest Landscape by Wildlife Alliance using animals confiscated from the illegal wildlife trade (Gray *et al*., 2017c).

Aside from the Siamese crocodile, few reptiles ranked highly in our assessments because these mostly scored poorly in the two most subjective criteria: ecosystem service values and charisma. Opportunities for rewilding nevertheless exist, most notably in the case of elongated tortoise and Asian giant softshell turtle *Pelochelys cantorii*, two species categorized as Critically Endangered (Rhodin *et al*., 2018). Monitored releases of both species, particularly individuals from the captive population of elongated tortoises at ACCB, is possible. However, other protected landscapes which are currently better protected, such as the JW Concession inside Botum Sakor National Park (Gray *et al*., 2019), may provide better prospects for release in the near future given the ongoing and trade-driven threats to almost all Asian chelonians (Rhodin *et al*., 2018).

Given our stated goals for rewilding in WSPWS combined with the results of our analysis, we recommend that initial rewilding efforts in the landscape focus on a subset of the mammals and reptiles identified. Species-specific feasibility studies should be conducted prior to any rewilding efforts however and there are likely to be significant hurdles associated with mitigating threats and improving protected area management across WSPWS. Having considered the present analysis, Rising Phoenix Co. Ltd., a social enterprise established to support conservation of WSPWS through partnership with government and development of a long-term financing strategy, has begun implementing the following measures. First, a commitment has been made to expand enforcement to reduce levels of gun-hunting and snaring via training, professionalization of management protocols, and increased numbers of enforcement rangers. Second, Rising Phoenix anticipates fencing of at least part of the protected area boundary to regulate human access and prevent the entry of domestic dogs. Allied to this, a PhD student from the University of Queensland is presently undertaking research on the distribution and habitat preferences of Eld's deer and the extent of predation by domestic dogs. Taken together, these will provide a comprehensive foundation for restoration of the species in WSPWS.

Gray *et al.* (2017a) argued that rewilding projects and reintroduction of iconic species in Cambodia, particularly tigers, could catalyse political and financial support for landscape-scale conservation. However iconic and charismatic species would be critical for this to occur and few taxa match the appeal of tigers or Asian elephants. Given the likely role of large grazers such as water buffaloes in structuring ecosystems, we recommend that rewilding in WSPWS begin with serious efforts to create large feral domestic water buffalo herds inside the protected area. If suitable riverine stretches can be found and targeted enforcement achieved, the conditions required for Siamese crocodile release could be achieved. Most of the other species that ranked highly in our analysis would require more detailed planning and feasibility studies to mitigate threats and determine sourcing options and conservation benefits of such projects (e.g., Eld's deer). Despite a number of challenges, we believe that rewilding will become an increasingly important conservation tool in Southeast Asia and our assessment represents the first attempt to identify appropriate candidates for rewilding efforts in the region's forests.

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Diversity of aquatic insect families and their relationship to water quality in urban ponds in Phnom Penh, Cambodia

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មូលន័យសង្ខេប

សត្វល្អិតទឹកត្រូវបានគេប្រើប្រាស់ជាសូចនាករជីវសាស្ត្រគុណភាពទឹកទាំងនៅក្នុងប្រព័ន្ធទឹកធម្មជាតិ និងពាក់កណ្តាលធម្មជាតិ។ ទោះជាយ៉ាងនេះក្តី ការសិក្សាបែបនេះគឺនៅមានកម្រិតនៅឡើយនៅក្នុងបរិស្ថានទីក្រុងនៃព្រះរាជាណាចក្រកម្ពុជា។ យើងបានធ្វើការសិក្សាពីជីវិតសត្វល្អិតទឹក និងទំនាក់ទំនងរបស់ពួកវាទៅនឹងគុណភាពទឹកនៅក្នុងត្រពាំងទឹកចំនួន៥ ក្នុងបរិវេណសាកលវិទ្យាល័យភូមិន្ទភ្នំពេញក្នុងប្រទេសកម្ពុជា។ សត្វល្អិតទឹកសរុបចំនួន៧,៣៥០ក្បាលស្ថិតក្នុង ២៣អំបូរ និង៦លំដាប់ត្រូវបានប្រមូល និងកំណត់អត្តសញ្ញាណដល់កម្រិតអំបូរ។ លំដាប់ Hemiptera (ភាគច្រើនជាអំបូរ Micronectidae) គឺមានវត្តមានលើសលប់នៅក្នុងសំណាកទាំងអស់ ចំណែកឯអំបូរ Ephemeroptea និងLepidoptera គឺមានវត្តមានតិចតួចជាងគេ។ ចំនួនប្រភេទ ចំនួនឯកត្ត: និងតម្លៃនានាភាព (Shannon-Wiener) មានភាពខុសគ្នាដាច់រវាងត្រពាំងទឹកដែលបានសិក្សា។ ចំនួនប្រភេទ និងចំនួនឯកត្ត:របស់សត្វល្អិតទឹកត្រូវបានរកឃើញច្រើនជាងគេនៅក្នុងត្រពាំងទឹក២ (P2 និងP4) ដែលមានទីតាំងនៅភាគអាគ្នេយ៍នៃសាកលវិទ្យាល័យភូមិន្ទភ្នំពេញ។ កត្តានេះអាចមកពីត្រពាំងទាំងពីរនោះមានគុណភាពទឹកល្អ និងមានរុក្ខជាតិទឹកច្រើន។ ត្រពាំងទឹក P5 ដែលមិនបានទ្រទ្រង់ជីវិតសត្វល្អិតច្រើននោះ មានរងនូវការបំពុលទឹក ព្រមទាំងសម្បូរទៅដោយពពួកសត្វល្អិតក្នុងអំបូរ Micronectidae និង Chironomidae ដែលជាពពួកសត្វល្អិតធន់នឹងការបំពុល។ លទ្ធផលនៃការវិភាគបានបង្ហាញថា ចំនួនប្រភេទ និងចំនួនឯកត្ត: របស់សត្វល្អិតទឹកគឺមានទំនាក់ទំនងជាវិជ្ជមានជាមួយនឹងកម្រិតអុកស៊ីសែនរលាយក្នុងទឹក ក៏ប៉ុន្តែវាមានទំនាក់ទំនងជាអវិជ្ជមានជាមួយនឹងកម្រិតកករនៅក្នុងទឹក។ ជាអនុសាសន៍ កិច្ចខិតខំប្រឹងប្រែងស្តារឡើងនូវគុណភាពទឹកនៃត្រពាំងដែលរងការបំពុលខ្លាំងនោះគួរតែត្រូវបានធ្វើឡើង ដើម្បីធ្វើឲ្យជីវិតក្នុងទឹកត្រពាំងមានភាពសម្បូរបែបឡើងវិញ។

Abstract

Aquatic insects are commonly used as bioindicators of water quality in semi-natural and natural aquatic systems. However, such studies are still limited in urban environments in Cambodia. We investigated aquatic insect life and its relationship to water quality in five ponds located on the grounds of the Royal University of Phnom Penh in Cambodia. A total of 7,350 individuals of aquatic insects belonging to 23 families and six orders were collected and identified to family level. Hemiptera (mostly Micronectidae) were most abundant in our samples overall whereas Ephemeroptera and Lepidoptera were the least abundant. Taxonomic richness, abundance and Shannon-Wiener's diversity values

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differed significantly between our study ponds. Two ponds (P2 and P4) located in the southeast portion of the university were found to support the highest taxonomic richness and diversity, which was likely due to better water quality and greater aquatic vegetation. The least diverse study pond (P5) had rather polluted water and was dominated by members of the Micronectidae and Chironomidae which are more tolerant to pollution. Regression analysis showed that aquatic insect richness and abundance were positively associated with dissolved oxygen levels, but negatively associated with water turbidity. We recommend that restoration efforts be undertaken to improve the water quality of the most polluted of our study ponds to enhance their aquatic life.

Keywords Invertebrate diversity, Diptera, dissolved oxygen, Hemiptera, Ephemeroptera, water turbidity.

Introduction

Aquatic insects (animals without an internal skeleton) are an ecological and polyphyletic group of arthropods which live or spend part of their life cycle in water (Pennak, 1978; Arimoro & Ikomi, 2008). Some species are entirely aquatic whereas others are semi-aquatic, and they collectively comprise 12 orders and approximately 100,000 species in total (Dijkstra *et al*., 2014). Aquatic insects are important in aquatic systems because they play major roles as consumers, detritivores, predators and/or pollinators (Balian *et al*., 2008).

Aquatic insects are commonly used as indicators of water quality in lentic and lotic systems because changes in the physical and chemical properties of water can strongly influence their presence and abundance (Uherek & Pinto, 2014). As such, their differing levels of tolerance to the amount and type of pollution can indicate different water quality classes (Cairns & Pratt, 1993; Kamsia *et al*., 2008). For example, the presence of most species in the orders Ephemeroptera, Plecoptera, and Trichoptera can indicate good water quality (Sor *et al*., 2017), because most of these taxa are sensitive to poor water quality and thus often occur in pollution-free systems (Bonada *et al*., 2006; Merritt & Cummins, 2008; Hamid & Rawi, 2011). On the other hand, some species belonging to the Odonata and Diptera orders can tolerate moderate to extremely polluted waters, respectively (Merritt & Cummins, 2008; Al-Shami *et al*., 2010; Hepp *et al*., 2013).

Anthropogenic activities such as releases of sewage, industrial and household water, coupled with run-off from agriculture and mining activities have reached a critical level in many aquatic systems in Asia (Prommi & Payakka, 2015; IPBES, 2018). As such, most waterbodies in the region are experiencing increasing pollution loads which are undoubtedly altering their physical-chemical properties e.g., temperature, dissolved oxygen, pH, conductivity, alkalinity, phosphates, nitrates, turbidity, and metal concentrations (Prommi & Payakka, 2015). Variations in these properties can greatly influence the distribution of aquatic insects because some taxa are highly sensitive to pollution and environmental disturbance, whereas others are moderately to highly tolerant (Hepp *et al*., 2013).

The diversity of aquatic insects in Cambodia and their relationships to water quality in urban aquatic systems is poorly studied to the best of our knowledge. We therefore aimed to investigate this in a well-known area of Phnom Penh, namely at the Royal University of Phnom Penh (RUPP). Specifically, we aimed to i) determine how diverse aquatic insects are in ponds at the RUPP, ii) identify which ponds are more or less vulnerable to pollution and consequently support a higher or lower aquatic insect diversity, and iii) quantify the relationship between aquatic insect diversity and specific water quality variables. We consequently provide baseline data regarding aquatic insect diversity and surface water quality at the Royal University of Phnom Penh.

Methods

Study area

Our study was carried out at five ponds located on the grounds of the RUPP which encompasses approximately 21 ha in Sangkat Teklark 1, Khan Toul Kork, Phnom Penh (between 11°34.0’N,104°53.3’E and 11°34.3’N, 104°53.6’E) (Fig. 1). The ponds at the RUPP provide a water source for aquatic organisms and valuable cultural services to the public and whereas some ponds receive wastewaters, others do not. We assumed these differences would likely influence the aquatic communities present.

Our first study pond (P1, Fig. 1) occupied the southwest corner of the RUPP grounds. Its waters were moderately clear during our study and surrounded by trees. Our second study pond (P2) was located in the southeast portion of the RUPP, in front of the Institute of Foreign Languages. Aquatic vegetation was more abundant within the pond and its waters were rather clear and clean. Our third study pond (P3) was situated in the northeast corner of the RUPP and surrounded by only a few trees. The pond had limited aquatic vegetation and its waters were dark-green, moderately turbid and pungent, with much plastic waste present. Our fourth study pond (P4) was located in front of the Cambodia-Japan Cooperation Centre in the southeast corner of the RUPP grounds. This appeared to be rich in aquatic vegetation, with clear waters. Our final study pond (P5) was located next to the Cambodia-Korea Cooperation Centre in the central-west portion of the RUPP. Aquatic and riparian vegetation were limited at the pond and its waters were turbid because the pond receives wastewater from the surrounding area.

Sampling design and data collection

Our sampling was undertaken between 18–20 January 2019. Four samples were obtained from different locations in each pond, providing a study total of 20 samples.

Aquatic insects were sampled at each location using an aquatic hand-net, which had an opening that measured 30 x 30 cm, a length (or depth) of 92 cm and a mesh size of 1 mm. This was used to collect aquatic insects near the shoreline for a total of 30 minutes at each pond. While this sampling method is biased towards natatonic and neustic organisms, it can also sample opportunistically benthic insects such as Chironomidae and was standardised at each pond.

Following collection, insects were placed on a white tray and rinsed with water for sorting and screening. These were then transferred with forceps into labelled containers containing 75% ethanol. Large insects were sorted by naked eye, whereas smaller individuals were sorted using a dissecting microscope (Olympus SZ61). The sorted material was later identified to family level using keys provided by Dudgeon (1999), Yule & Yong Hoi (2004) and Burnhill (2006).

Several water quality variables were measured at each sampling location using a HI-7609829 Multiparameter Portable Water Quality Meter (Hanna Instruments Ltd., Bedfordshire, UK). These included pH, water temperature, dissolved oxygen, electrical conductivity, turbidity, and total dissolved solids. All measurements were made between 0.1–0.5 m in water depth, after sampling for aquatic insects.

Data analysis

We calculated taxonomic richness (=the number of taxa), abundance (=the number of individuals), and Shannon-Wiener's diversity index (H) values for each sampling location and pond (Hamid & Rawi, 2017; Sor *et al*., 2017). We also quantified the total number of individuals per taxon. As a non-parametric distribution was assumed due to the small sample size for each pond, Kruskal-Wallis tests were employed to test for significant differences in the taxonomic richness, abundance and diversity values between the ponds.

To assess relationships, these community metrics were regressed against our water quality data, which were normalized using the zero minimum (Sor *et al*.,

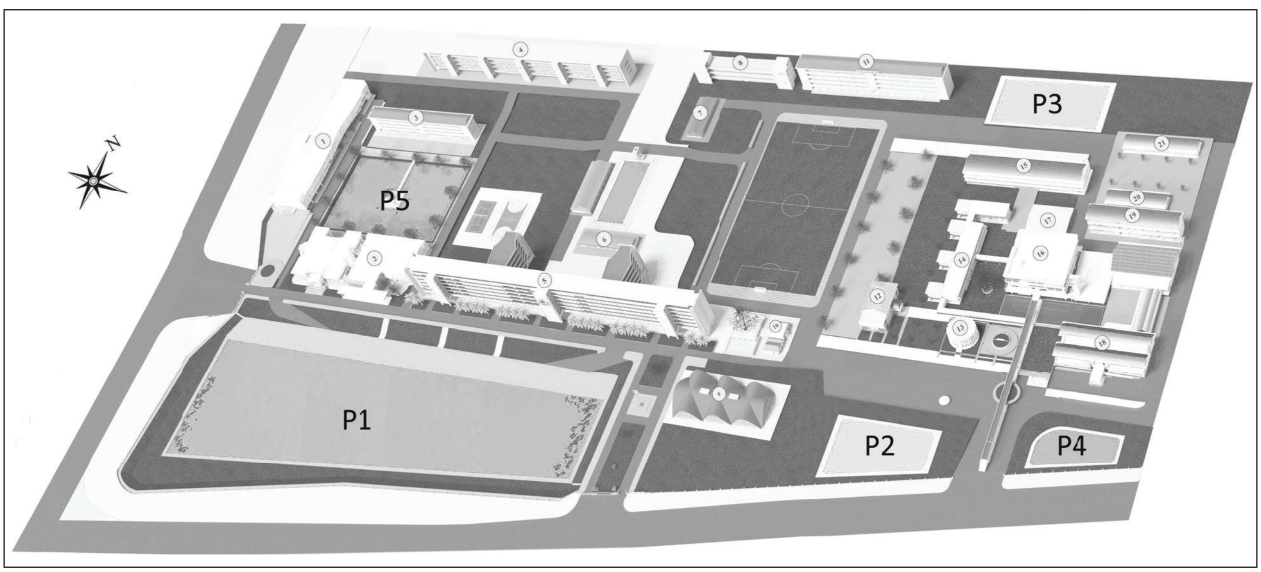

Fig. 1 Location of five study ponds (P1–P5) on the grounds of the Royal University of Phnom Penh (© RUPP Faculty of Engineering).

2017). An overall multiple linear regression was first employed to this end. All water quality variables that proved significant in these tests were then individually tested again against the community metrics using either simple or multiple regression. Values of $P<0.05$ were considered significant in all tests and all analyses were performed in the R statistical environment (R Core Team, 2018).

Results

Overall diversity

We collected and identified a total of 7,350 individuals arranged in 23 families and six orders (Annex 1). The most diverse and abundant order in our study material was Hemiptera with eight families: Micronectidae (5,676 individuals), Notonectidae (216), Vellidae (208), Nepidae (132), Belostomatidae (108), Gerridae (52), Hydrometridae (28), and Pleidae (1). This was followed by Odonata with five families: Coenagrionidae (98), Protoneuridae (77), Libellulidae (73), Corduliidae (1), and Gomphidae (1). The order Coleoptera was represented by members of the Hydrophilidae (75), Hydroscaphidae (67), Dytiscidae (1), and Gyrinidae (1), whereas the order Diptera was represented by members of the Chironomidae (573), Culicidae (85), Stratiomyidae (39), and Tabanidae (3). Ephemeroptera and Lepidoptera were the least abundant orders and represented by members of the Baetidae (10) and Crambidae (5), respectively. The taxonomic richness, abundance and diversity of our study material is summarised along with water quality variables in Table 1.

Aquatic insect diversity between ponds

The aquatic insect communities of our study ponds differed significantly in taxonomic richness (H=9.67, P=0.046), abundance (H= 11.53, P=0.021) and diversity (H=11.54, P=0.021) (Fig. 2).

Study ponds 2 and 4 had the greatest values for taxonomic richness (11.5±1.7 and 10.8±2.7 respectively), followed by pond 5 (8±2.7), pond 1 (7.3±3.8), and finally, pond 3 (4.8±2.9). With respect to abundance, pond 5 had the greatest number of individuals (1,600±2,087), followed by pond 4 (80±28), pond 2 (71±27), pond 1 (52±28), and finally, pond 3 (36±41). In terms of diversity, study ponds 2 and 4 again showed the greatest values (with a mean H value of 1.94±0.21 and 1.87±0.47 respectively), followed by pond 1 (1.46±0.44), pond 3 (0.88±0.79), and finally, pond 5 (0.77±0.55).

Relationship between aquatic insects and water quality

Our metrics for aquatic insects were significantly associated with just two water quality variables: turbidity and dissolved oxygen (Table 2). Taxonomic richness and abundance were negatively associated with turbidity, whereas taxonomic richness was significantly and positively associated with dissolved oxygen (Fig. 3, Table 2).

Discussion

Our study appears to be the first report on aquatic insects in urban areas in Cambodia. However, as we were only able to identify insect taxa to family level, the species diversity and composition of our study sites remains

Table 1 Summary of water quality values and community metrics recorded at five study ponds in the grounds of the Royal University of Phnom Penh.

Variable/Metric (unit)	Minimum	Maximum	Mean	Standard deviation
Temperature (°C)	28.4	31.2	29.7	0.9
Dissolved oxygen (%)	39.2	177.5	82.8	39.8
Electrical conductivity (mS/m)	78	526	292.9	161.5
Turbidity (FNU)	8.7	116	44.6	33.0
pH	7.5	9.3	8.2	0.6
Total dissolved solids (mg/L)	39	263	146.6	80.7
Taxonomic richness (taxa/sample)	1	14	8.5	3.6
Abundance (individuals/sample)	9	4684	367.5	1043.2
Shannon-Weiner diversity (H)	0	2.3	1.4	0.7

unknown. Although only 23 families arranged in six orders were documented, our study nonetheless contributes to knowledge of aquatic insects in urban areas in Cambodia. Relatively few studies have been conducted on aquatic insects in the country to date (e.g., Kosterin & Chartier, 2014; Kosterin, 2015a, 2015b; Zettel *et al*., 2017; Freitag *et al*., 2018) and fewer still have investigated the relationship between these and water quality and other environmental variables (e.g., Sor *et al*., 2017, 2018).

Among the 12 orders of aquatic insects, Hemiptera and Diptera have been reported as most abundant in lentic (still water) systems, whereas Ephemeroptera, Plecoptera, and Trichoptera are the least abundant (Balian *et al*., 2008). Our results are consistent with this finding as Hemiptera was the most commonly found order. This is likely because hemipterans can tolerate low concentrations of dissolved oxygen and high turbidity because various families in the order have different methods of replenishing air stores, including plastron respiration (Kurzatkowska, 2003; Chen *et al*., 2015). This may explain why Micronectidae was the most abundant family in study pond 5, which had turbid and polluted waters. Similarly, the paucity of Ephemeroptera in our study likely reflects the fact that most taxa in the order prefer unpolluted waters and running waters (Collier & Lill, 2008; Sor, 2017; Sor *et al*., 2017).

We found that study ponds 2 and 4 in the southeast portion of the RUPP grounds supported the highest taxonomic richness and diversity values for aquatic insects (Fig. 2). This may be because both ponds are characterised by diverse aquatic vegetation (including algae, water lilies, and water grass) and surrounding trees that provide good conditions for shelter and foraging and refuges from predators (Andersson, 2014). Many aquatic insect taxa thrive in undisturbed habitats (Mohd *et al*., 2012) and changes in habitat quality (e.g., substrate composition, water quality, and physical conditions) can substantially influence their diversity. Study pond 1 supported comparatively lower diversity, which could be partly due to the reduced amount of aquatic vegetation present, whereas ponds 3 and 5 had the lowest diversity scores of all. The latter may be due to the fact that these ponds function as reservoirs which receive wastewater

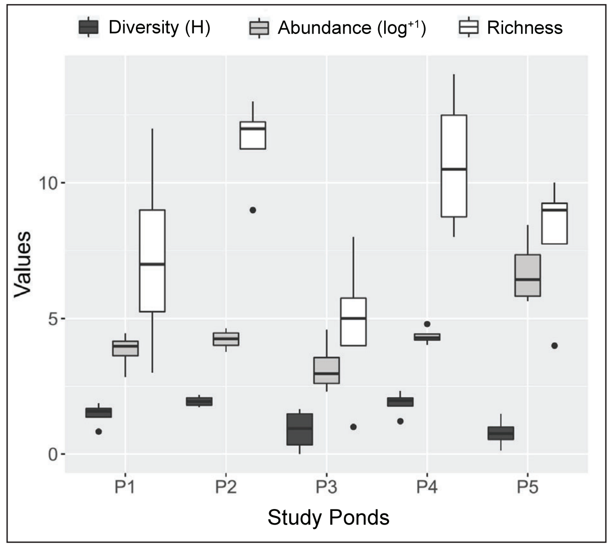

Fig. 2 Box and whisker plots of values for Shannon-Wiener's diversity (H), abundance, and taxonomic richness of aquatic insects in five study ponds. Rectangles show the first and third quartiles, dark bars represent medians, whereas the lower and upper ends of vertical lines represent minimum and maximum values and dots represent outliers.

Table 2 Linear regression models of community metrics and water quality variables recorded at the Royal University of Phnom Penh. Asterisks indicate that only variables that had significant relationships with community metrics (in overall multiple linear regression against all variables recorded) were employed.

Linear models	Co-efficient	Adjusted R^2	*F* statistic	*P* value
Simple*				
Taxonomic richness ~ turbidity	-7.22	0.355	11.46	0.003
Abundance ~ turbidity	0.13	-0.546	0.02	0.901
Abundance ~ dissolved oxygen	2.58	0.161	4.64	0.045
Multiple (abundance ~ turbidity + dissolved oxygen)*	-	0.49	10.17	0.001
~ Turbidity	-4.68	-	-	-
~ Dissolved oxygen	6.33	-	-	-

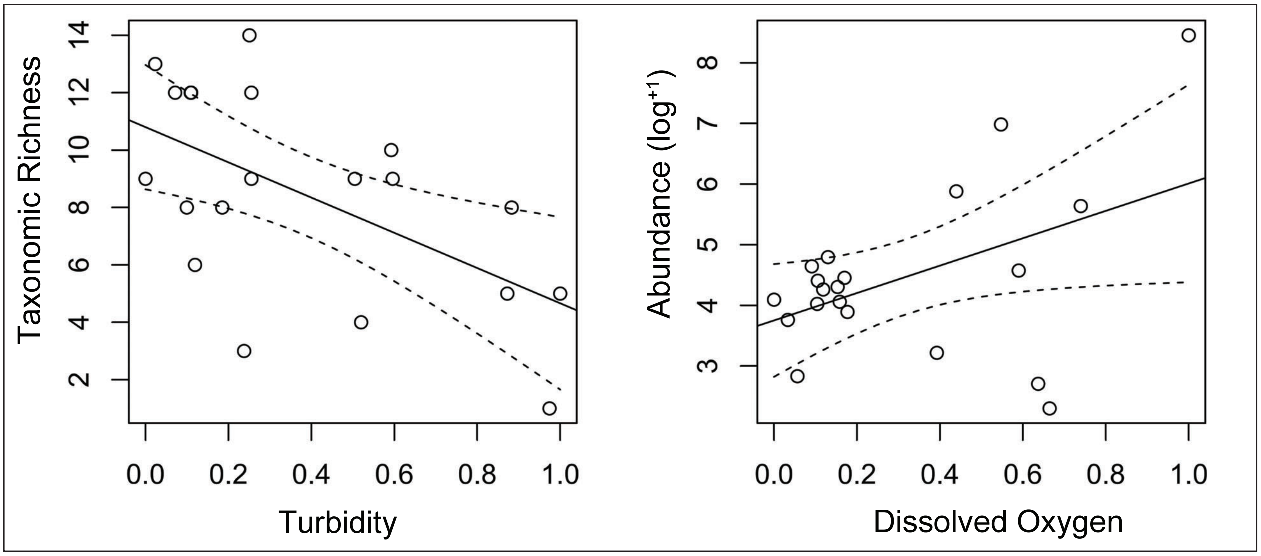

Fig. 3 Simple linear regression of the aquatic insect community metrics (taxonomic richness and abundance) and normalized water quality variables (turbidity and dissolved oxygen). Dashed-lines represent lower and upper 95% confidence intervals.

from the university and are thus more polluted. The lack of surrounding trees and aquatic vegetation at the two ponds may exacerbate this. However, our data suggest that the aquatic insect fauna of pond 3 is somewhat healthier than pond 5, which was highly dominated by members of the Micronectidae and Chironomidae, both of which are more tolerant of pollution (Slooff, 1983).

Among the water properties we tested, dissolved oxygen was the major variable which had a positive relationship with aquatic diversity in our study. This is consistent with the results of studies elsewhere, including the Mekong region in Asia (Sor *et al*., 2017), New Zealand (Collier & Lill, 2008), and Europe (Królak & Korycińska, 2008). In contrast, water turbidity had a strong negative relationship with the taxonomic richness and abundance of aquatic insects. Limited richness and abundance of Ephemeroptera, Plecoptera and Trichoptera has been observed in highly turbid water bodies elsewhere for example (Hershey *et al*., 2010) and it may be that water turbidity indirectly influences aquatic insects because high levels of turbidity can affect dissolved oxygen regimes (van Heest *et al*., 2005). Factors which increase water turbidity include sediments induced by algae blooms, soil erosion and pollutants in industrial wastewater and sewage discharges (van Heest *et al*., 2005; Ebenebe *et al*., 2016). With respect to our study ponds, we recommend restoration efforts be undertaken to improve the water quality and surrounding environments of ponds 3 and 5.

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Annex 1 Aquatic insects and water quality variables recorded at the Royal University of Phnom Penh.

Water quality values represent mean (min–max). Asterisks indicate taxa that occurred in only one location and for which only one water quality measurement is therefore provided.

Order/Family	Abundance	Occurrence	pH	Dissolved oxygen (mg/L)	Electrical conductivity (m/L)	Total dissolved solids (mg/L)	Turbidity (FNU)	Temperature (°C)
Hemiptera								
Nepidae	132	14	8.1 (7.5-9.3)	71.4 (39.2-131.1)	260.6 (79.0-526.0)	130.4 (39.0.-263.0)	36.1 (8.7-94.1)	29.7 (28.4-31.2)
Gerridae	52	10	8.0 (7.5-8.6)	63.5 (39.2-100.0)	255.7 (78.0-525.0)	127.9 (38.9-262.0)	30.7 (10.7-84.1)	29.6 (28.4-31.2)
Notonectidae	216	13	8.4 (7.7-9.3)	91.3 (39.2-177.5)	311.2 (78.0-526.0)	155.7 (39.0-263.0)	48.7 (10.7-94.1)	30.02 (28.4-31.2)
Belostomatidae	108	16	8.2 (7.5-9.3)	85.04 (39.2-177.5)	323.2 (79.0-526.0)	161.7 (39.0-262.0)	47.1 (10.7-116.0)	28.9 (27.9-31.0)
Vellidae	28	6	8.2 (7.5-9.3)	73.6 (53.8-120.8)	320.3 (155.0-408.0)	160.3 (78.0-204.0)	45.07 (18.0-84.1)	29.4 (28.3-30.4)
Micronectidae	5,676	8	8.3 (7.7-9.3)	109.4 (55.6-177.5)	406.9 (78.0-526.0)	203.5 (39.0-263.0)	63.33 (17.2-116.0)	29.8 (28.4-30.5)
Hydrometridae	28	4	7.6 (7.5-7.7)	55.8 (51.8-60.4)	287.5 (161.0-330.0)	144 (81.0-165.0)	25.5 (10.7-30.5)	29.1 (28.4-31.2)
Pleidae*	1	1	8.6	62.7	79.0	39.0	18.1	28.9
Diptera								
Chironomidae	573	13	8.2 (7.7-9.3)	87.3 (39.2-177.5)	299.4 (78.0-526.0)	149.8 (39.0-263.0)	44.9 (8.7-117.0)	29.0 (27.9-31.0)
Stratiomyidae	39	9	7.8 (7.7-8.4)	63.3 (39.2-114.9)	297.0 (155.0-526.0)	148.7 (78.0-263.0)	28.5 (8.7-59.6)	29.7 (28.4-31.2)
Tabanidae	3	3	7.8 (7.7-8.1)	57.3 (53.6-61.1)	245.7 (78.0-330.0)	123.0 (39.0-165.0)	25.9 (17.2-30.5)	28.8 (28.4-29.4)
Culicidae	85	2	8.1 (7.7-8.4)	138.8 (100.0-177.5)	518.5 (512.0-525.0)	259.0 (256.0-262.0)	55.6 (51.8-59.3)	30.4 (30.2-30.6)
Odonata								
Libellulidae	73	14	8.0 (7.5-8.6)	67.3 (39.2-177.5)	236.1 (78.0-526.0)	118.1 (39.0-263.0)	25.9 (8.7-59.6)	29.5 (28.4-31.1)
Corduliidae*	1	1	7.7	57.2	330.0	165.0	30.1	28.5
Gomphidae*	1	1	7.7	57.2	330.0	165.0	30.1	28.5
Protoneuridae	77	8	8.03 (7.7-8.6)	53.7 (39.2-63.7)	149.9 (78.0-329.0)	75.1 (38.9-165.0)	17.1 (8.7-30.5)	29.6 (28.3-31.1)
Coenagrionidae	98	11	7.9 (7.5-8.6)	71.5 (39.2-177.5)	249.3 (78.0-526.0)	124.7 (38.9-263.0)	26.5 (8.7-59.6)	29.4 (28.4-31.2)
Ephemeroptera								
Baetidae	10	5	8.1 (7.8-8.4)	75.6 (39.2-177.5)	212.8 (79.0-512.0)	106.6 (38.9-256.0)	22.4 (8.7-51.8)	30.4 (28.7-30.6)
Coleoptera								
Dytiscidae*	1	1	8.6	62.7	79.0	39.0	18.1	29.0
Hydrophilidae	75	13	8.0 (7.5-8.6)	80.2 (39.2-177.5)	341.0 (155.0-526.0)	170.6 (78.0-263.0)	41.4 (8.7-116.0)	29.7 (28.4-31.2)
Hydroscaphidae	67	10	8.1 (7.7-9.3)	63.3 (39.2-120.8)	247.9 (79.0-408.0)	124.1 (38.9-204.0)	32.3 (8.7-84.1)	29.7 (28.4-31.2)
Gyrinidae*	1	1	7.5	60.4	330.0	165.0	30.5	28.4
Lepidoptera								
Crambidae	5	5	8.02 (7.7-8.6)	65.1 (51.8-100.0)	250.0 (79.0-525.0)	125 (39.0-262.0)	27.24 (10.7-59.3)	29.8 (28.5-31.2)

Discovery of the genus *Hidari* Distant, 1886 (Lepidoptera: Hesperiidae: Hesperiinae) in Cambodia and life cycle of *Hidari bhawani* de Nicéville [1889]

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មូលន័យសង្ខេប

អត្ថបទនេះមាននិយាយអំពីវត្តមាននៃសត្វមេអំបៅពីរប្រភេទ ស្ថិតក្នុងពួក*Hidari* (ដោយ Distant ឆ្នាំ១៨៨៦) ដែលជាកំណត់ត្រាដំបូងសម្រាប់ប្រទេសកម្ពុជា គឺៈ មេអំបៅស្លឹកដូង (*Hidari irava*) ដោយ Moore ឆ្នាំ១៨៥៨ និងមេអំបៅមានទ្រនង់លើស្លាបជាប់គ្នា (*Hidari bhawani*) ដោយ de Nicéville ឆ្នាំ១៩៨៩។ ការពិពណ៌នាអំពីដំណាក់កាលមិនទាន់ពេញវ័យនៃ *H. bhawani* (ស៊ុត ដង្កូវ និងដឹកឌឿ) រុក្ខជាតិធ្នូលរបស់វា និងលក្ខណៈលំអិតនៃការលូតលាស់ និងការវិវត្តន៍មួយចំនួនត្រូវបានបង្ហាញ។

Abstract

This paper documents the occurrence of two species of the genus *Hidari* Distant 1886 for the first time in Cambodia: coconut skipper *Hidari irava* (Moore, [1858]) and veined palmer or cresentric skipper *Hidari bhawani* de Nicéville [1989]. Descriptions of the immature stages of *H. bhawani* (egg, larvae, and pupa), its host plant and some details of life history are provided.

Keywords Host plant, *Licuala spinosa*, new country record.

Introduction

The genus *Hidari* Distant, 1886 contains three species: coconut skipper *H. irava* (Moore, [1858]), veined palmer or cresentric skipper *H. bhawani* de Nicéville, [1989], and long-spotted skipper *H. doesoena* Martin, 1895. *Hidari irava* has a wide distribution and has been recorded in South Myanmar, Thailand, Malaysia, Sumatra, Java, Sulu Archipelago (Philippines), Borneo, and Banka (India) (Evans, 1949). It has also been recorded near to Cambodia in the Chanthaburi and Trat provinces of Thailand (Pinratana, 1985). *Hidari bhawani* has been recorded in the Arakan Coast (Myanmar), Toungoo (Myanmar), Lakhimpur (India), Assam (India), Langkawi Island (Malaysia) (Evans, 1949), Rayong Province (Thailand) (Ek-Amnuay, 2012), and Dong Nai Province (Vietnam) (Monastyrskii & Devyatkin, 2015). *Hidari doesoena* is known from Sumatra, Batoe Island, Sipora Island (Indonesia), Kinabalu (Malaysia) (Evans, 1949), Ranong (Peninsular Thailand) (Ek-Amnuay, 2012), and Thua Thien Hue (north-central Vietnam) (Monastyrskii & Devyatkin, 2015).

Hidara ivara is common in Thailand and one of the most common Malayan hesperiids. *Hidara bhawani* is rare in Thailand and very rare in Peninsular Malaysia. *Hidara doesoena* is also rare in Thailand and much rarer than *H. irava* in Peninsular Malaysia (Corbett & Pendlebury, 1992; Ek-Amnuay, 2012).

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Robinson *et al.* (2010) listed the following host plants for *H. irava*: *Bambusa* spp. (Gramineae), *Arenga* spp., *Caryota urens*, *Cocos nucifera*, *Elaeis guineensis*, *Livistona* spp., *Metroxylon* spp. (including *M. sagu*), and *Nypa* spp. (including *N. fruticans*) (Palmae). Igarashi & Fukuda (1997) also listed Musaceae as host plants for the species. Robinson *et al*. (2010) and Ek-Amnuay (2012) did not include host plant information for *H. bhawani* or *H. doesoena*, although Corbett & Pendlebury (1992) suggested that the latter probably feeds on jungle palms. Aside from this vague comment, no mention of the larvae or host plant of *H. doesoena* appears in the literature.

The larva of *H. irava* is pale yellowish-green with a dark brown lateral stripe (Corbett & Pendlebury, 1992). The larvae spin a bag-like nest with two neighbouring leaves, in which 2–3 larvae live. These feed at night and are usually found about 1–2 m above the ground and the final instar reaches approximately 60 mm in length (Igarashi & Fukuda, 1997). The pupa is a shiny reddish to blackish-brown colour with a dark brown lateral line and is covered in white powder (Corbett & Pendlebury, 1992; Igarashi & Fukuda, 1997).

The mangrove fan palm *Licuala spinosa* Wurmb is widespread in Southeast Asia, occurring in the Andaman Islands, Borneo, Cambodia, Myanmar (Tanintharyi), Peninsular Malaysia, Philippines, Sumatra, Thailand, and Vietnam (Henderson, 2009). Its habitats include lowland rain forest in low wet places, savanna, scrub forest, and disturbed land up to 600 m in elevation (Henderson, 2009).

Robinson *et al*. (2010) did not list any lepidopteran species whose larvae use *L. spinosa* as a host plant. However, a blog post (Han, 2011) documents the use of *L. spinosa* as the larval host plant by the yellow streak darter *Salanoemia tavayona* (Evans, 1926), another skipper which is rare in neighbouring Thailand (Ek-Amnuay, 2012) and Peninsular Malaysia (Corbett & Pendlebury, 1992).

The present paper documents the first records of *H. bhawani* and *H. irava* from Cambodia and presents the first details of the life history of *H. bhawani*. The *Hidari* genus was previously unrecorded in Cambodia and the life history of *H. bhawani* was also undescribed.

Methods

The study area was located in the Tatai Kraom Commune, Koh Kong District of Koh Kong Province (Fig. 1). The author has recorded observations of fauna and flora in this area on many occasions over the last decade. Most of these observations have focused on a ca. 5 ha area (indicated in yellow in Fig. 1 and centering on 11.580°N, 103.128°E), but all areas outlined in red in Fig. 1 have been visited many times. All evidence for Lepidoptera was based on photography alone, due to the lack of local storage facilities for lepidopteran specimens.

Identification of *Hidari* species was undertaken using keys in Evans (1949). The genus was first established as follows: FW origin of vein 5 nearer vein 4 than vein 6 (Ea); hindwing cell normal (Fa); antennal club not restricted before the apiculus and vein 5 well marked (Fb); palpi second segment erect (Ha); antennal apiculus finely pointed (Ia); HW vein 5 not decurved at origin and wings produced (J); hindwing cell not abnormally long (J.1a); antennal apiculus longer than twice width of club, hooked or obtuse; palpi third segment not protruding (J.12a); F cell very long ≥ dorsum (J.19a); antennae not > ½ costa (J.19b); FW vein 5 decurved (J.20a); HW cell = ½ wing; apiculus hooked; UpF with yellow hyaline spots; spot in space 1b (J.20).

The two species were identified as follows:

- UpF hyaline yellow spot in space 2 not reaching origin of vein 3: central spots in spaces 2, 3 and cell separate and equidistant (J.20.1a).
- UnF pale brown with more or less well-developed small brown, whitish centred, spots; UnH, with a small pale spot near upper end of cell (J.20.1a.I = *H. irava*).
- UnF pale brown tessellated with dark, brown dashes; UnH with small·discal spots as in *irava*, no pale cell spot, but with a more or less developed brown streak under·vein 8 (J.20.2 = *H. bhawani*).

The immature stages of *H. bhawani* were studied by collecting and observing one larva (Larva A) on 26 May 2015 (at 11.581°N, 103.128°E), plus three eggs and one larva (Larva B) on 23 July 2019 (at 11.518°N, 103.143°E). The eggs and larvae were checked at least once a day and photographed to document their stage of development.

The identity of the host plant was determined using keys in Henderson (2009). The genus was first determined as follows: leaves palmate (1); leaf blades divided into leaflets (2b); hastulas present (4b); leaf sheaths fibrous, not split at base (6b); petiole margins with thorns (10a); leaflets split to their bases into multi-fold, wedge-shaped leaflets with lobed apices (11a = *Licuala*).

The relevant parts of the key for species of *Licuala* in Henderson (2009) are purely based on geography, with those for Cambodia (1b, 2b, 4b, 7b, 11a: Henderson, 2009) indicating *L. spinosa*. As such, the parts of the key that referred to the neighbouring region of Thailand were also considered due to its proximity to the study area

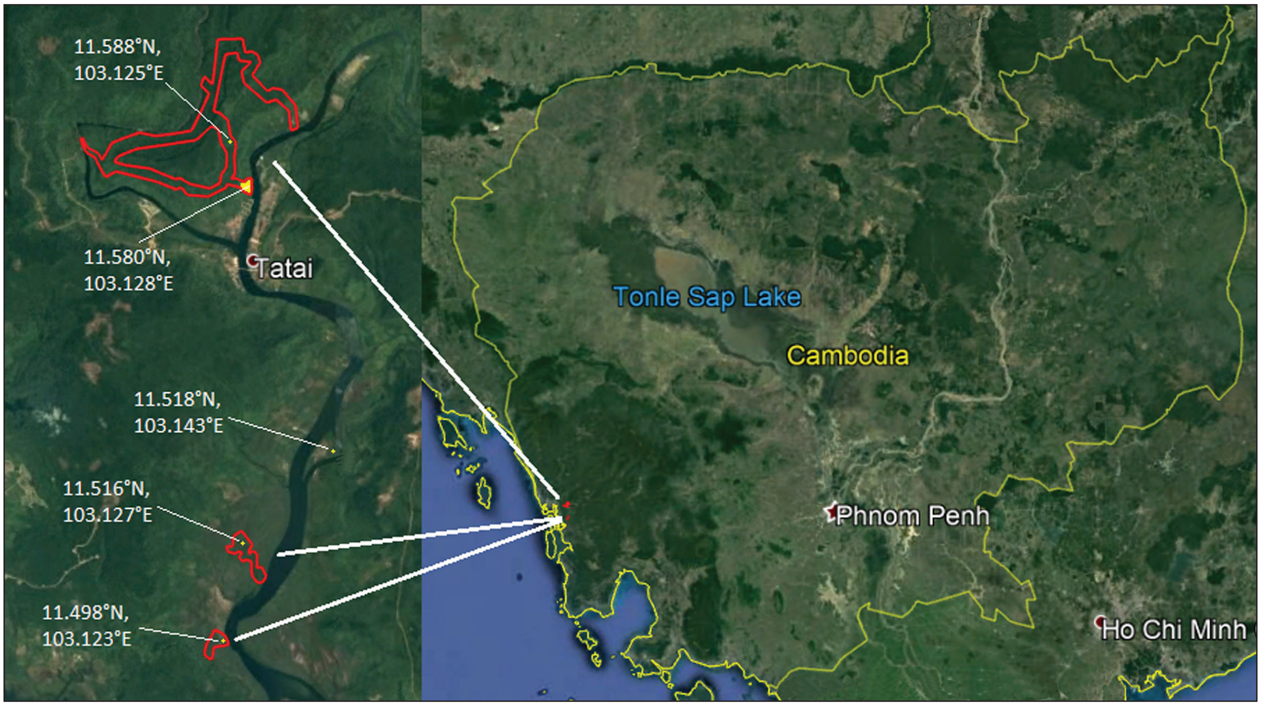

Fig. 1 Study areas in Tatai Kraom Commune, Koh Kong District, Koh Kong Province, southwest Cambodia.

(11b, 12a, 13a: Henderson, 2009). The specific diagnosis comprised: stems forming large clumps of equal-sized stems; petiole thorns stout, to 1.2 cm, borne all along the petioles (14a = *Licuala spinosa*). This was confirmed in personal communication with Andrew Henderson.

Taxonomic placement of Lepidoptera is based on Beccaloni *et al*. (2018). No tribes are given therein for any hesperiid mentioned here due to current uncertainties regarding tribal relationships within some clades of Hesperiinae (Warren *et al*., 2009).

Photographs were taken with three different cameras. Photographs were taken in 2012 and 2013 using a Canon EOS 500D with a 55-250 mm lens, whereas in 2015 these were taken using a Panasonic DMC-FZ200 and in 2019 with Olympus TG-4, fitted with FD-1 flash diffuser.

GPS coordinates were recorded with the Olympus TG-4 camera from June 2016 onwards, whereas coordinates for earlier photographs were estimated using Google Earth. All coordinates are given as latitude/longitude degrees in decimal format to three decimal places.

Approximate measurements of the eggs, larvae and adult of *H. bhawani* were made using a handheld tape measure. These were estimated from photographs taken of subjects together with the tape measure.

Results

Observations of adults of genus *Hidari*

Photographs were obtained of adults of *H. irava* (Fig. 2A) on 24 separate occasions between March 2011 and October 2018. These were observed in all months from February to November and at times ranging from 06:18 to 21:08 hrs. Twenty-three of the observations were in the yellow region marked in Fig. 1 (11.580°N, 103.128°E), whereas the remainder occurred in the northernmost location (11.588°N, 103.125°E). Most observations were made in shady secondary growth and scrubby areas, but occasional sightings of adults were also made indoors after dark or very early in the morning, these being presumably attracted by lights.

Photographs were obtained of adults of *H. bhawani* (Fig. 2B) on seven separate occasions (excluding adults reared from larvae) between June 2012 and July 2019. Observations were made in March, May, June, and July, and at times ranging from 05:56 to 18:03 hrs. Four observations occurred in the yellow region marked in Fig. 1 (11.580°N, 103.128°E), whereas the remainder were at the three marked points (11.518°N, 103.143°E; 11.516°N, 103.127°E; 11.498°N, 103.123°E). Six sightings were in similar habitats to those of *H. irava*, with two of the seven photographs taken indoors. One adult was photographed

Fig. 2 A) *Hidari irava,* adult, B) *H. bhawani,* adult, C) *H. bhawani,* egg ca. 24 hrs after oviposition, D) *H. bhawani,* first instar and egg, E) *H. bhawani,* first instar making its shelter, F) *H. bhawani,* leaf damage from first instar, G) *H. bhawani,* first instar with frass, H: *H. bhawani,* first instar during moulting, I) *H. bhawani,* second instar, J) *H. bhawani,* penultimate instar during moulting, K) *H. bhawani,* final instar, L) *H. bhawani,* final instar, fully evacuated prior to pupation, M) *H. bhawani,* prepupa, N) *H. bhawani,* pupa, O) *H. bhawani,* leaf damage from final instar, P) *H. bhawani,* final instar eating, Q) Habitat where *H. bhawani* eggs and Larva B were collected, R) Habitat where Larva A of *H. bhawani* was discovered.

ovipositing on a very small (only 10 petioles) individual of *L. spinosa* in a small area of vegetation in the middle of plastic decking at a resort on the river island of Koh Andet (Fig. 2Q). Some nearby habitat is similar to that where the other sightings were made, particularly across the narrow (approximately 20 m) stretch of river directly in front of the resort.

Life history of *H. bhawani*

Little can be said about the development of Larva A because it was a late final instar when collected. However, comparative remarks on this and other larvae reared are given further below.

On 23 July 2019 (day 1), one day after oviposition was observed, eight eggs and one larva (Larva B) were found. Three of the eggs were collected and the chronological development of these and Larva B are detailed separately below.

Eggs, Day 1: Six of the eggs were on separate leaf segments and the remaining two were on the same segment. One of the eggs was on the tubular shelter of Larva B. The eggs were pale, creamy-orange in colour with a pinkish-red top and irregular line, the same pinkish-red, around the middle but with its ends not meeting. The eggs were almost hemispherical, but flat or slightly indented dorsally, with 20–21 ribs (Fig. 2C), ca. 1.7 mm in diameter.

Day 2: Two of the eggs had changed to become more uniform creamy-pink in colour. This change did not occur to the third egg until day 4. This failed to hatch and was later discarded.

No observation was made on day 3.

Day 4: Two larvae (Larva C and Larva D) had hatched the previous night. Each was creamy-yellow in colour with a dark brown head and had a thin, dark brown dorsal line at the base of the abdomen (Fig. 2D). These were approximately 5 mm in length. Little remained of the eggs, the rest having presumably been eaten by the larvae. The larvae had already made shelters in folds of the leaf segments and made new shelters (Fig. 2E) within 30 minutes of breaking the original shelter. By evening, Larva C had darkened to almost black.

Day 5: By early morning, Larva C had grown to a little over 6 mm in length (Fig. 2G) and become more green in colour, presumably in part from the green food showing through its translucent body. Its frass was also green (Fig. 2G). Larva D had not grown and was still yellow in colour. Despite the presence of tiny amounts of frass which showed that it was eating, larva D failed to grow and was dead by day 8.

Day 6–9: Larva C grew to ca. 8 mm by the evening of day 6. By the evening of day 7, it had developed a whitish lump behind its head and had begun moulting. The white lump increased in size in the morning of day 8 (Fig. 2H) and moulting was complete that evening. There was little difference between the first and second instar. The head was a paler brown colour and there was no dorsal line at the base of the abdomen (Fig. 2I). By the end of day 9, Larva C had grown to 10 mm in length.

Day 10: Larva C had left its leaf and was on the plastic container. This was the only time the larva was seen away from its leaf. Some minutes later, Larva C had liquid around it and died that evening. It appeared to have a lesion in its side.

Larva B, Day 1: Larva B was found in a tubular shelter formed by the folds of a leaf segment and was in the process of moulting when collected (Fig. 2J). The following morning, it was ca. 38 mm long (Fig. 2K). Its head was grey in colour and bordered with black, with four black spots. Two large spots were almost central to each half of the anterior portion of the head, whereas two smaller spots were conjoined in the posterior portion. The body had less colour and was more transparent than earlier instars, revealing more of the internals of the larva, including lateral white trachaeae originating ventrally and spreading dorsally. In captivity, Larva B created a tubular shelter similar to the one in which it was found.

Day 2–8: Larva B showed no changes in appearance, apart from growing to a length of 46 mm.

Day 9–10: Larva B had changed colour, with no hint of green by the morning (Fig. 2L). It frass had also changed from loosely-packed and pale brown to appearing harder and much darker (almost black). By evening, the larva began to prepare for pupation (Fig. 2M). It sealed itself within a much narrower shelter in the folds of its leaf segment. Its colour was slightly darker and becoming less yellow. The head appeared to be already dislocated. There was a white powdery substance on the leaf and around the prolegs of the larva. The prepupa was 40 mm in length. By the following morning (day 10), body colour had darkened to an almost uniform tan, but was darker at the end of the abdomen, and there was also slightly more white powder. Its length had reduced to 35 mm.

No observations were possible on day 11.

Day 12–22: The pupa had formed by the morning of day 12 (Fig. 2N). This was a light golden-brown colour which darkened towards its anterior and the remains of the head were still attached to the posterior end of the pupa. The pupa appeared to be shiny and smooth beneath the white powder with which it was lightly dusted and was ca. 28 mm long, excluding the remains of the head. No further changes were noted in the pupa up to and including day 21, but by the evening of day 22, it had darkened to almost black.

Day 23: The adult (a female) had already emerged and its wings were fully expanded by the morning (Fig. 2B). Its length was ca. 13 mm, from tip of the labial palps to the end of the abdomen. The length of the forewing from base to apex was ca. 24 mm.

Remarks on Larva A, B and C

Larva A was discovered in secondary scrub (Fig. 2R), which included several *L. spinosa* among a mixture of plants including unidentified small trees, bamboo and palms (including snake fruit *Salaca* sp.). The plant which Larva A was feeding on was at the edge of a small clearing where a small house stood. This was collected in its feeding tube (Fig. 2O) where it was first observed eating from the apex of the leaf (Fig. 2P). Larva B ate in a similar manner in captivity. However, Larva C differed, eating instead from the side of the leaf segment (Fig. 2F).

Larva A was slightly different from Larva B in appearance, as the two clear, black, and conjoined spots on the head of the latter were barely visible on the former. Larva A alone also had a pair of pale parallel stripes running dorsally along its body. The morning after collection, Larva A had already begun preparations for pupation, having eaten its entire shelter between collection at 16:50 hrs and 07:16 hrs. The time from preparations for pupation to emergence of the adult (a male) was 12 days for Larva A, whereas it was 14 days for Larva B.

When disturbed in nature, Larva A exhibited defensive behaviour which consisted of retreating into its tubular shelter. In captivity, Larva B differed: if touched, it trashed its head from side to side and made an audible clicking noise, both of which would continue for up to a minute.

Discussion

The discovery of *Hidari* spp. in Cambodia is not surprising. *Hidari irava* is very common and has been recorded close to the study area in the neighbouring Trat and Chanthaburi provinces of Thailand (Pinratana, 1985). *Hidari doesoena* and *H. bhawani* have also been recorded in locations on either side of Cambodia, in Thailand and Vietnam (Ek-Amnuay, 2012; Monastyrskii & Devyatkin, 2015).

The location of the oviposition site observed in 2019 (Fig. 2Q) was unexpected. *Licula spinosa* is a very common in the area and frequently grows in secluded places that are less disturbed by humans. Despite this, the skipper chose a very open location frequented by people, this being directly between the bar and restaurant of a popular resort. This was similar in some ways to the location of the *L. spinosa* individual chosen by the skipper in 2015. This was located on the edge of a clearing less than 10 m from the authors house, despite the presence of several *L. spinosa* in more secluded locations nearby.

It seems paradoxical that while *H. bhawani* is a very rare skipper, its host plant (*L. spinosa*) is abundant in the study area. Although *L. spinosa* plants were examined on multiple occaisions in several locations during the period between the two study collections (26 May 2015 and 23 July 2019), no further evidence of *H. bhawani* or other lepidopteran larvae was observed. However, a similar scenario (i.e. a rare skipper using *L. spinosa* as a larval host plant) has been reported for *S. tavoyana* (Han, 2011) and it is possible that the development cycle is rarely successful. Of the three eggs collected in this study, none produced an adult skipper. However, the results of captive-rearing efforts may not necessarily apply to development in a natural environment.

Little can be said about the breeding habits of *H. bhawani* from this study. What is clear is that breeding was recorded in both May and July. It is also apparent that either multiple adult females oviposit on the same plant or a single adult oviposits on the same plant on more than one occasion. This is demonstrated by the simultaneous presence of newly laid eggs and a penultimate instar on the same plant.

The larval habits of *H. bhawani* observed in this study differ from those reported for *H. irava*. For example, *H. irava* has been reported to feed at night (with no mention of daytime feeding) and to make a feeding shelter by joining two leaves together, with 2–3 larvae sharing the same shelter (Igarashi & Fukuda, 1997). In contrast, the individuals observed in this study made tubular shelters from single leaf segments, fed during the day (observed at 13:36 and 17:47 hrs), and remained solitary in their feeding shelters. However, given the quantity of leaf consumed by Larva A during the brief and mostly overnight period it spent in its container before pupation, it would seem likely that *H. bhawani* also feeds at night.

Acknowledgements

The author thanks Tek Lin Seow and Les Day for help with butterfly identification, Oleg Kosterin for kindly reviewing the content of this paper and several anonymous reviewers for their very constructive comments.

Thanks are also due to Alexander Monastyrski and Andrew Henderson for clarifying several points in this paper and to Anna Carangian Pawlik for allowing the author to cut her *L. spinosa* plants to collect butterfly material and photograph the site.

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Short Communication

Rediscovery of the Critically Endangered giant land snail *Bertia cambojiensis* (Reeve, 1860) in Cambodia

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The phylum Mollusca contains the second highest number of species after the phylum Arthropoda. Land snails belong to the most diverse class (Gastropoda) in the phylum which comprises three main groups: shell-snails, shell-less slugs, and intermediate semi-slugs (Schilthuizen, 2017). Land snails are shelled snails which require calcium carbonate ($CaCO_3$) for growth and production of egg shells (Mand *et al*., 2000; Uchidal *et al*., 2013). Dyakiidae comprise large and medium-sized land snails belonging to 12 genera, including three that are sinistral. One of these, *Bertia* Ancey, 1887, is endemic to eastern Indochina and has three recognized species (Thach, 2015; Sutcharit *et al*., 2019). *Bertia* was initially described as a monotypic genus based on *Helix cambojiensis* Reev, 1860 due to its very large and sinistral, helicoid shell (Sutcharit *et al*., 2019). This has the largest diameter of any land snail shell in Southeast Asia (Schileyko, 2016).

Once thought to be extinct, the giant land snail *B. cambojiensis* is currently listed as Critically Endangered (Naggs, 2014) and has hitherto only been recorded in the present-day territory of Southern Vietnam (Naggs, 2014; Schileyko, 2011; Sutcharit *et al*., 2019) (Fig. 1). As high-levels of deforestation are occurring in the region (Warren-Thomas *et al*., 2018), further information is required to improve understanding of its population status and enable monitoring and conservation actions. We document the first records of *B. cambojiensis* in Cambodia and describe the morphology of individuals encountered relative to descriptions provided by Schileyko (2011).

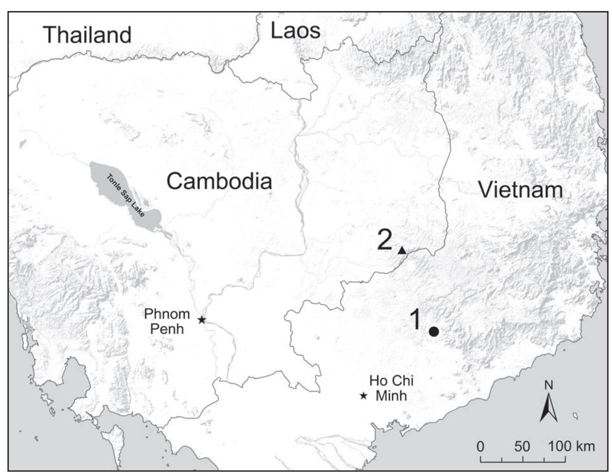

Fig. 1 Records for B. *cambojiensis* in Southeast Asia: 1) Cat Tien National Park (Sutcharit *et al*., 2019), 2) Keo Siema Wildlife Sanctuary (this study).

CITATION: Hun S., Samorn V., Ith S. & Chan B. (2019) Rediscovery of the Critically Endangered giant land snail *Bertia cambojiensis* (Reeve, 1860) in Cambodia. *Cambodian Journal of Natural History*, **2019**, 128–130.

In November 2018, four live individuals and a 14 empty shells of *B. cambojiensis* were encountered in O'Reang District, Mondulkiri Province (12°18″N, 107°05″E) (Fig. 1). This area forms part of the Keo Seima Wildlife Sanctuary (KSWS) which was declared in 2016 and is managed by the Cambodian Ministry of Environment (Evans & Delattre, 2005; WCS, 2016). Keo Seima Wildlife Sanctuary supports a rich biodiversity, including 34 globally threatened vertebrate species and at least five primate species (Pollard *et al*., 2008). The climate of the area is tropical monsoonal with a dry season from November to April and a wet season from May to October (WCS, 2016). Total annual rainfall varies between 2,200–2,800 mm, >85% of which occurs during the wet season (WCS, 2016). Hundreds of seasonal grassy wetlands and natural ponds occur within the sanctuary, as do two tributaries which drain into Dong Nai River in Southern Vietnam.

Following sightings, live snails were kept in suitable habitats to encourage them to emerge from their shells for photography. Specimens of live individuals and empty shells were preserved and later deposited in the Zoological Collection of the Centre for Biodiversity Conservation at the Royal University of Phnom Penh, Cambodia. Morphological characters were measured using a digital calliper.

Bertia cambojiensis (Reeve, 1860)

Diagnosis: The species is characterised by a sinistral, helicoid shell which has a black and red-brown base encircled by a broad white band. A narrow dark brown stripe with a helical shape is present along the suture edge of body whorl and broadens close to the lip (Fig. 2).

Description: Sinistral helicoid shell, width greater than height. Shell height ranges from 49.9–56.6 mm and shell width from 80.5–85.1 mm (*n*=16). Aperture relatively smaller than *B. setzeri*, deep spiral umbilicus, cone shape spire with blunt protoconch. Live animals have a light orange foot and dark brown eyes.

Habitat: *B. cambojiensis* was observed in evergreen forest in KSWS. During our survey in the early dry season of November, live snails were sighted on the dry ground in leaf litter ≤20 metres from a stream with water. Others were found in shade under logs and fallen trees. Shells were also found in forest away from the stream.

Fig. 2 Views of *B. cambojiensis* specimen collected in the Keo Siema Wildlife Sanctuary, eastern Cambodia.

Remarks: The geographical range of *B. cambojiensis* is poorly known and despite its presumed occurrence in Cambodia, the species was hitherto recorded only from a small area in Southern Vietnam (Naggs, 2014; Sutcharit *et al*., 2019) (Fig. 1). As *B. cambojiensis* is Critically Endangered, our confirmation of its occurrence in a protected area in eastern Cambodia is welcome news for conservation management. However, habitat loss likely presents a threat to the species. Further, as we observed many empty shells of *B. cambojiensis* outside houses in KSWS that were evidently discarded after cooking, harvesting for local consumption may also present a serious threat. Further surveys are consequently recommended to improve understanding of the distribution, ecology, and conservation status of the species in Cambodia.

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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. Lead 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.

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New species & taxonomic reviews

Bayarsaikhan, U., Im K.-H. & Bae Y.-S. (2019) Two new species and a newly recorded species of the genus *Stictane* Hampson (Lepidoptera, Erebidae, Arctiinae) from Cambodia. *Zootaxa*, **4686**, 253–263.

The authors describe two species of moth new to science (*Stictane heppneri* sp. nov. and *S. transversana* sp. nov.) based on specimens collected in the Koh Kong, Kampot and Siem Reap provinces. They also document the first record of *S. obscura* in Cambodia and provide an identification key for *Stictane* species in Cambodia, with figures of adults and genitalia. Author: baeys@inu.ac.kr

Grismer, L.L., Wood, P.L., Quah, E.S.H., Anuar, S., Poyarkov, N.A., Neang T., Orlov, N.L., Thammachoti, P. & Hun S. (2019) Integrative taxonomy of the Asian skinks *Sphenomorphus stellatus* (Boulenger, 1900) and *S. praesignis* (Boulenger, 1900) with the resurrection of *S. annamiticus* (Boettger, 1901) and the description of a new species from Cambodia. *Zootaxa*, **4683**, 381–411.

The authors revise the taxonomy of three species of *Sphenomorphus* skinks based on phylogenetic, morphological and colour pattern data and describe one species new to science from Phnom Chi in Prey Lang Wildlife Sanctuary: *S. preylangensis* sp. nov. Author: lgrismer@lasierra.edu

Hosoishi S. (2019) A new subterranean *Crematogaster* with one ommatidium from Cambodia, based on morphology and DNA (Hymenoptera, Formicidae). *Acta Entomologica*, **59**, 507–511.

The author describes a new species of mymicine ant to science based on two worker specimens collected in leaf litter in lowland forest in Koh Kong Province. The new species is named *Crematogaster monocula* and is morphologically similar to *C. masukoi* of the *C. biroi* group. Author: hosoishi@gmail.com

Jager, P. (2019) *Selenops ef* sp. nov. (Araneae: Selenopidae) from Cambodia: first record from an Asian cave. *Arachnology*, **18**, 245–247.

The author describes a species of spider new to science (*Selenops ef* sp. nov.) from Battambang Province, which represents the first record of the genus from a cave in Asia. A distribution map is given for *Selenops* species in Asia and the cave-dwelling habit of the new species is discussed. Author: peter.jaeger@senckenberg.de

Ko J.-H., Lee T.-G., Bayarsaikhan, U., Park B.-S. & Bae Y.-S. (in press) Review of genus *Cirrhochrista* Lederer, 1863 (Lepidoptera: Crambidae: Spilomelinae) from Cambodia, with the first description of the male of *Cirrhochrista fuscusa*. *Journal of Asia-Pacific Biodiversity*. DOI 10.1016/j.japb.2019.09.008

The authors review the genus *Cirrhochrista* in Cambodia, which comprises six newly-recorded species. Photographs of adults and genitalia are provided, with re-descriptions, collection data and information on the distribution and host plants of each species. Author: baeys@inu.ac.kr

Kosterin, O.E. (2019) Description of a female and variation of *Microgomphus alani* Kosterin, 2016 (Odonata: Gomphidae) in Cambodia, with a note on sexual dimorphism in *Microgomphus* spp. *Zootaxa*, **4701**, 276–290.

The author describes morphological variation in new specimens of the recently discovered *Microgomphus alani* in Cambodia, namely a male and two females from Phnom Kulen (Siem Reap Province) and five females and one male from Mondulkiri Province. Author: kosterin@bionet.nsc.ru

Kovarik, F. & Stahlavsky, F. (2019) Revision of the genus *Reddyanus* from Southeast Asia, with description of five new species from Cambodia, Malaysia, Thailand and Vietnam (Scorpiones: Buthidae). *Euscorpius—Occasional Publications in Scorpiology*, **295**, 1–45.

The authors describe five species of *Reddyanus* scorpion new to science, including two from Cambodia: *R. rolciki* sp. nov. and *R. schwotti* sp. nov. Details of karyotypes are presented alongside descriptions of external morphology. An identification key and distribution map for the 14 species of *Reddyanus* recognised by the authors in Southeast Asia are also included.

Vermeulen, J.J., Luu H.T., Theary K. & Anker, K. (2019) Land snail fauna of the Mekong Delta limestone hills (Cambodia, Vietnam): *Notharinia* Vermeulen, Phung et Trung, 2007, and a note on *Plectostoma* A. Adams, 1865 (Mollusca: Gastropoda: Caenogastropoda: Diplommatinidae). *Folia Malacologica*, **27**, 167–177.

The authors present a revision of the mollusc genus *Notharinia*, which includes 10 species that are endemic to limestone hills on the western flank of the Mekong River delta in Vietnam and Cambodia. Seven of the 10 species are described as new to science, including four from Cambodia: *N. constricta* sp. nov., *N. lyostoma* sp. nov., *N. soluta* sp. nov., and *N. stenobasis* sp. nov. Author: jk.artandscience@gmail.com

Biodiversity inventories

Kosterin, O.E. (2019) Occasional photographic records of butterflies (Lepidoptera, Hesperioidea and Papilionoidea) in Cambodia. 2. Ratanakiri and Mondulkiri Provinces of Eastern Cambodia, 2013–2018. *Acta Biologica Sibirica*, **5**, 21–37.

The author presents opportunistic records of 123 butterfly species (including five provisionally identified species) from 33 localities in the Ratanakiri and Mondulkiri provinces between 2013 and 2018. These include the first records for Cambodia of 19 butterfly species and one subspecies. Author: kosterin@bionet.nsc.ru

Species ecology & status

Heinrich, S., Ross, J.V., Gray, T.N.E., Delean, S., Marx, N. & Casseya, P. (2020) Plight of the commons: 17 years of wildlife trafficking in Cambodia. *Biological Conservation*. DOI 10.1016/j.biocon.2019.108379

The Wildlife Rapid Rescue Team (WRRT) of the Cambodian Forestry Administration has combatted wildlife trafficking in Cambodia since 2001. The authors analysed confiscation records of the WRRT for 2001–2018 to determine compositional trends in trafficked species and identify conservation gaps. Birds comprised the highest number of animals confiscated, although reptiles accounted for the greatest number of confiscation incidents. The authors show that Cambodia contributes substantially to the bird trade and may be an under-reported element of the Asian songbird crisis. Author: sarah.heinrich@adelaide.edu.au

Coasts, wetlands & aquatic resources

Baird, I.G. & Green, W.N. (2019) The Clean Development Mechanism and large dam development: contradictions associated with climate financing in Cambodia. *Climatic Change*. DOI 10.1007/s10584-019-02621-4

The Clean Development Mechanism (CDM) of the Kyoto Protocol was designed to reduce greenhouse gas emissions and promote sustainable development, but has financed hydropower dams that have caused serious environmental and social impacts. The authors consider the case of the Lower Sesan 2 (LS2) dam in northeast Cambodia. While the LS2 has not received funding from the CDM, it could be registered to receive post-construction financing. The authors highlight an apparent lack of improvements in critical areas of the CDM despite years of criticisms and suggest there are framing and structural issues which make reform difficult. This is timely because the CDM is scheduled to end in 2020, after which it will be replaced by a new and currently unspecified climate change financing mechanism. Author: ibaird@wisc.edu

Fiorella, K.J., Bageant, E.R., Kim M., Sean V., Try V., MacDonell, H.J., Baran, E., Kura Y., Brooks, A.C., Barrett, C.B. & Thilsted, S. (2019) Analyzing drivers of fish biomass and biodiversity within community fish refuges in Cambodia. *Ecology and Society*, **24**, 18.

Freshwater systems are shaped by site-specific characteristics, environmental change and annual fluctuations, and the actions of resource users and managers. The authors assessed the influence of these factors on the fishery productivity and biodiversity of 40 rice field fisheries (community fish refuges) over three years and found that seasonal and site-specific effects relate strongly to biomass and species richness patterns within these systems. They also found an association between biomass and biodiversity and some elements of governance capacity building. Their findings suggest that management actions for rice field fisheries that are tailored and responsive to local contexts may be most appropriate given the strong inter-annual and site-specific drivers.

Pool, T., Elliott, V., Holtgrieve, G., Aria, M., Altman, I., Kauman, L., McCann, K., Fraser, E.D.G., Tudesque, L., Chevalier, M., Grenouillet, G., Chea R., Lek S., McMeans, B., Cooperman, M., Chheng P., Hannah, L., Miller, B., Chuanbo G. & So N. (2019) Fish assemblage composition within the floodplain habitat mosaic of a tropical lake (Tonle Sap, Cambodia). *Freshwater Biology*. DOI 10.1111/fwb.13391

Effective conservation of flood–pulse catchments requires an understanding of how habitat heterogeneity is linked to biodiversity patterns in these systems. The authors evaluated whether mesohabitat-scale (1–5 km) factors throughout the floodplains of the Tonle Sap Lake affect fish assemblages temporally and spatially. They conclude that fish assemblage structure and floodplain mesohabitat use within the lake may depend strongly upon maintaining the natural flow regime. Author: poolt@seattleu.edu

Forests & forest resources

Chim K., Tunnicliffe, J., Shamseldin, A. & Ota T. (2019) Land use change detection and prediction in upper Siem Reap River, Cambodia. *Hydrology*. DOI 10.3390/hydrology6030064

The Siem Reap River has played an important role in maintaining the Angkor temple complex and livelihoods of people in the basin since the 12th century. As land use in the surrounding watershed has changed in recent decades and possibly influenced the river, the authors reconstructed annual deforestation patterns from 1988 to 2018 and explored land use scenarios 40 and 80 years into the future. Their results suggest that forest cover in the watershed has declined by 1.22% annually over the last three decades, and that a continued downward trend in forest cover can be expected in the future. Author: chimkosal@yahoo.com

Coad, L., Lim S. & Nuon L. (2019) Wildlife and Livelihoods in the Cardamom Mountains, Cambodia. *Frontiers in Ecology and Evolution*, **296**, 1–18.

The authors assessed the use of wild meat and fish in three village communities in the northern Cardamom Mountains through household interviews and group discussions. Their results suggest that >80% of households hunt and >90% fish, but also suggest that arable farming provides the bulk of incomes. The authors conclude that while wildlife-friendly farming initiatives may support livelihoods and promote conservation, continued declines in biodiversity are likely without stricter enforcement of wildlife trade laws in urban areas and reduction of demand for wildlife products in consumer countries. Author: lauren.coad@me.com

Kaura, M., Arias, M.E., Benjamin, J.A., Oeurng C. & Cochrane, T.A. (2019) Benefits of forest conservation on riverine sediment and hydropower in the Tonle Sap Basin, Cambodia. *Ecosystem Services*. DOI 10.1016/j.ecoser.2019.101003

Hydropower development has accelerated in the Mekong region and recent deforestation rates in Cambodia are among the world's highest. Forest protection represents a service to hydropower because forest loss accelerates erosion which increases river sediments and decreases hydropower production. The authors evaluated four proposed medium-size hydropower dams and found that these could lose 60–100% of their storage capacity over 120 years at current deforestation rates. They suggest that their approach is transferable to dams in other regions where hydropower development is accelerating and ecosystem services from surrounding watersheds require quantification. Author: mearias@usf.edu

Veettil, B.K. & Ngo X.Q. (2019) Mangrove forests of Cambodia: recent changes and future threats. *Ocean and Coastal Management*, **181**, 1–7.

Mangrove forests are important for coastal area protection, ecosystem services and other socio-economic purposes. The authors analysed satellite data to determine changes in mangrove cover in Cambodia and estimate that 42% of mangrove cover was lost between 1989–2017 in the Koh Kong, Kampot, Preah Sihanoukville provinces. However, they also suggest that mangrove loss has decreased in recent years due to reforestation, banning of illegal charcoal production and deactivation of non-profitable aquaculture ponds. Author: bijeeshkozhikkodanveettil@duytan.edu.vn

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

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.

The *Cambodian Journal of Natural History* publishes original work by:

- Cambodian or foreign scientists on any aspect of Cambodian natural history, including fauna, flora, habitats, management policy and use of natural resources.
- Cambodian scientists on studies of natural history in any part of the world.

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The following types of manucripts are accepted:

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- Research on the status or ecology of habitats.
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- Reviews of conservation policy and legislation in Cambodia.
- Conservation management plans for species, habitats or areas.
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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.

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Cambodian Journal of Natural History

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