

HABITAT PREFERENCES AND ACTIVITY PATTERNS OF THE LARGER MAMMAL COMMUNITY IN PHNOM PRICH WILDLIFE SANCTUARY, CAMBODIA

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ABSTRACT. – The northern and eastern plains of Cambodia support one of the largest extents of lowland deciduous forest in South-east Asia and are globally significant for mammal conservation. Between Dec.2008 and Aug.2009 intensive camera-trapping was conducted within mosaic deciduous dipterocarp and mixed-deciduous/semi-evergreen forest in the east of Phnom Prich Wildlife Sanctuary, Monduliri province, Cambodia. Forty camera-trap locations were set up for >2700 camera-trap nights producing 707 independent encounters of 23 mammal species. Eight globally threatened species of mammals were recorded including the Asian elephant (*Elephas maximus*), banteng (*Bos javanicus*) and dhole (*Cuon alpinus*). Two species, the gaur (*Bos gaurus*) and pig-tailed macaque (*Macaca nemestrina*), showed significant preference for forest type (higher Relative Abundance Index of both species in mixed-deciduous/semi-evergreen forest). The mix of drier deciduous dipterocarp forest and wetter mixed-deciduous and semi-evergreen forest appears important for maintaining the conservation value of the site. Camera trap encounter rates were lower in areas within a day's walk from villages at the periphery of the protected area whilst catemeral species displayed higher proportions of nocturnal activity than in similar studies from elsewhere in South-east Asia. We suggest disturbance and hunting may therefore be affecting the distribution and activity patterns of key species. Managing the Non Timber Forest Product (NTFP) collectors as well as finalising, and enforcing, zonation within the protected area are recommended conservation measures for the mammal community.

KEY WORDS. – Camera-trap; deciduous dipterocarp forest; wild cattle; human disturbance; Indochina.

INTRODUCTION

Northern and eastern Cambodia supports some of the largest extents of lowland deciduous forest in South-east Asia (Todorff et al., 2005). These forests were formerly described as one of the “great game-lands of the world; a Serengeti of Asia” and supported a diverse and abundant mega-fauna of ungulates, predators and scavengers (Wharton, 1957; Todorff et al., 2005). Despite recent local (e.g. the hog deer, *Axis porcinus*) and possible global extinctions (e.g. the kouprey, *Bos sauveli*) Cambodia’s northern and eastern plains remain globally significant for mammal conservation and support more than 30 International Union for Conservation of Nature (IUCN) listed species (Todorff et al., 2005). These include the Asian elephant (*Elephas maximus*), the tiger (*Panthera tigris*) and three species of wild cattle (the gaur, *Bos gaurus*; banteng, *B. javanicus*; and the wild water buffalo, *Bubalus arnee*) (World Wildlife Foundation (WWF)/Wildlife Conservation

Society (WCS), unpublished data). The lowland forests of north and east Cambodia typically comprise of a mosaic of dominant deciduous dipterocarp forest with smaller patches of semi-evergreen or mixed deciduous forest along water-courses and at slightly higher elevations. This mosaic of forest types may be essential for the survival of the large mammal community as a suite of species (e.g. some primates, Asian elephant and gaur) appear, at least seasonally, dependant on the wetter mixed deciduous and semi-evergreen forest (Todorff et al., 2005; Gray et al., 2010). These closed forests may also act as refugia or source populations for species more easily hunted in the open deciduous dipterocarp forest (Duckworth et al., 2005).

Unfortunately habitat preferences and activity patterns are poorly known for most terrestrial mammal species within Indochinese deciduous forests. This is particularly worrying for conservationists given the pervasive threats to biodiversity

throughout South-east Asia from habitat loss and hunting (Sodhi et al., 2004). Camera-traps are increasingly used by conservationists to inventory protected areas, determine species presence-absence, activity patterns and habitat preferences and to estimate relative, and absolute, abundance (Griffiths & van Schaik, 1993; Karanth & Nichols, 1998; Azad, 2006; Grassman et al., 2006; Gimán et al., 2007; McShea et al., 2009). Whilst camera-traps have limitations for surveying arboreal species (e.g., primates, squirrels, some civets and cats) the technique is particularly valuable for surveying low density, nocturnal, shy or otherwise elusive forest mammal species in areas where observations and unambiguous identification of signs are rare. This study uses camera-trapping to document the presence of larger terrestrial mammal species of conservation concern within Phnom Prich Wildlife Sanctuary, Mondulki Province, Cambodia and to examine their basic habitat preferences, activity patterns and responses to human activities within the protected area.

MATERIAL AND METHODS

Study area. – Phnom Prich Wildlife Sanctuary (henceforth PPWS) is located in the west of Mondulki Province, east Cambodia (centered on 12.8° N, 106.5° E) and covers 2225 km² (Fig. 1). The climate is highly seasonal with a cooler wet-season (July–November) and a hot, dry-season, in which precipitation is extremely rare (December–June). Terrain is characterised by higher elevation and relief (max. 640 masl) in the southeastern section near the Mondulki plateau, sloping down towards the north and west to gently undulating lowlands with elevation ca. 80–200 masl. PPWS consists of a mosaic of deciduous dipterocarp forest (henceforth DDF) (1027 km²) and wetter semi-evergreen/mixed-deciduous forests (henceforth SEGF) (1070 km²). The deciduous dipterocarp forests are typically dominated by one or more of five species of dipterocarpaceae: *Shorea siamensis*, *S. obtusa*, *Dipterocarpus tuberculatus*, *D. obtusifolius* and *D. intricatus* (Rundel, 1999). These forests, which experience a high frequency burning regime, generally consist of a single stratum of trees that are 5–12 m in height, creating a relatively open structure with 50–70% canopy cover and an extensive understory of grass or herbaceous bamboo. In contrast, mixed deciduous and semi-evergreen forests are wetter with typically taller canopy, less developed understory and are often dominated by *Lagerstoemia* spp. and *Hopea* spp. (Rundel, 1999).

Following the cessation of armed-conflict in the late 1990s biodiversity surveys identified PPWS as globally significant for mammal conservation particularly for wild cattle, elephants and large carnivores (Timmins & Ou, 2001). While no inventory of mammal species within PPWS has been published since camera-trapping between 2001 and 2005 did record 30 terrestrial mammal species, of which eight are globally threatened (WWF unpublished data).

Camera-trapping. – Between Dec.2008 and Aug.2009, we deployed commercially available infra-red, remote-trip digital camera units (Reconyx RapidFire Professional PC90;

WI, USA), in which all photographs were digitally stamped with date and time, in eastern PPWS. Camera-traps were placed at 40 locations (28 in DDF; 12 in SEGF; Fig. 1). The initial objectives of this study were to document the presence/absence of tiger and wild cattle, and cameras were, therefore, placed at locations designed to maximise chances of encountering these species. Seventeen camera-trap locations were along animal tracks, 13 beside vehicular roads and tracks and 10 along dry-stream beds. All cameras were placed on trees between 25–100 cm above the ground (mean = 47 cm). No two cameras were placed closer than 1 km from each other to achieve some form of spatial independence. Camera trapping effort (number of 24-hour operational camera trap nights) at each location was calculated from the date the camera was set until the date it was retrieved or, if cameras malfunctioned, until the date stamped on the final exposure. The number of camera trap nights per location varied between three and 119 (mean 67.9 ± SDEV 33). For all photo-captures of larger mammals (*sensu* Duckworth & Pine, 2003), the species, camera-trap location, date and time were recorded. Smaller mammals, not detected by cameras (e.g. shrews, bats, treeshrews) or not identifiable to species (e.g. rats), together with arboreal species (e.g. primates, squirrels) did not form part of this study.

Relative Abundance Indices (RAI) were calculated from the encounter rate of each species. RAI was defined as the number of independent photographs of each species per 100 camera-trap nights (O'Brien et al., 2003). Successive photographs of the same species were defined as independent

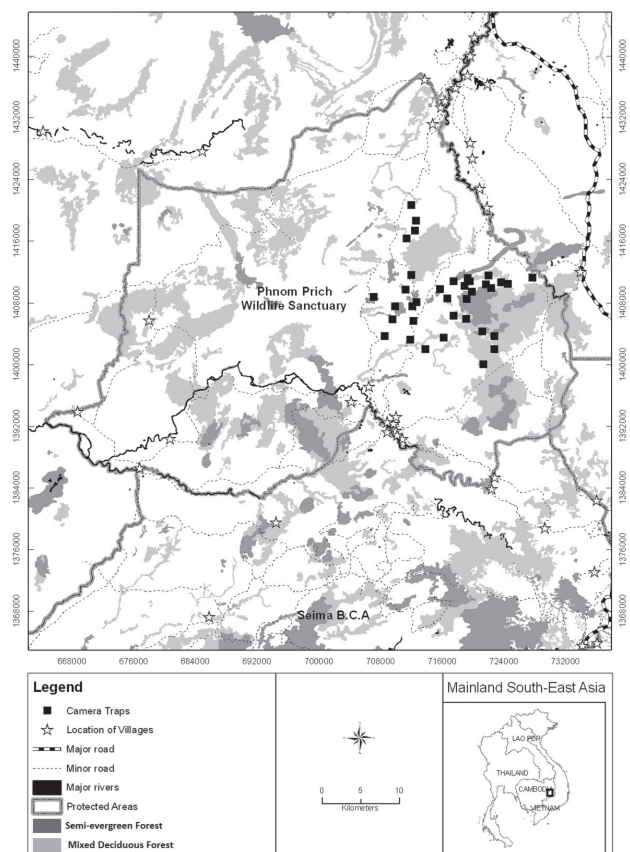


Fig. 1. Locations of camera-traps within Phnom Prich Wildlife Sanctuary, eastern Cambodia.

Table 1. Relative Abundance Index (RAI - independent encounters/100 trap nights) for larger mammal species within Phnom Prich Wildlife Sanctuary, number of locations each species recorded from (minimum 25 trap nights/trap location) and percentage of nocturnal (1800–0600) activity. Nocturnal, diurnal or cathemeral activity patterns indicated with n, d or c. Statistically significant patterns (two-tailed at $p < 0.05$) in upper case. IUCN status (EN Endangered; VU Vulnerable; NT Near Threatened) in parentheses. Species with more than nine encounters used in statistical analysis indicated with asterix.

Common name	Species	Encounters	RAI	No. # of locations	Nocturnal activity %
red muntjac*	<i>Muntiacus muntjak</i>	183	6.74	32	39 (C)
Eurasian wild pig*	<i>Sus scrofa</i>	155	5.70	30	57 (C)
Asian elephant (EN)*	<i>Elephas maximus</i>	84	3.10	20	69 (C)
banteng (EN)*	<i>Bos javanicus</i>	65	2.39	19	89 (c)
large Indian civet (NT)*	<i>Viverra zibetha</i>	45	1.66	16	96 (n)
east Asian porcupine*	<i>Hystrix brachyura</i>	36	1.32	14	100 (N)
common palm civet*	<i>Paradoxurus hermaphroditus</i>	23	0.85	13	95 (n)
leopard cat*	<i>Prionailurus bengalensis</i>	21	0.77	11	63 (C)
leopard (NT)*	<i>Panthera pardus</i>	20	0.74	11	47 (C)
dhole (EN)*	<i>Cuon alpinus</i>	17	0.63	9	19 (c)
pig-tailed macaque (VU)*	<i>Macaca nemestrina</i>	10	0.37	6	100 (D)
gaur (VU)*	<i>Bos gaurus</i>	9	0.33	6	75 (c)
Berdmore's squirrel	<i>Menetes berdmorei</i>	8	0.29	3	N/A
golden jackal	<i>Canis aureus</i>	7	0.26	3	N/A
small Indian civet	<i>Viverricula indica</i>	6	0.22	5	N/A
sun bear (VU)	<i>Ursus malayanus</i>	5	0.18	4	N/A
hog badger (NT)	<i>Actonyx collaris</i>	4	0.15	2	N/A
Siamese hare	<i>Lepus peguensis</i>	3	0.11	2	N/A
long-tailed macaque	<i>Macaca fascicularis</i>	2	0.07	2	N/A
yellow-throated marten	<i>Martes flavigula</i>	1	0.04	1	N/A
large spotted civet (VU)	<i>Viverra megaspilla</i>	1	0.04	1	N/A
clouded leopard (VU)	<i>Neofelis nebulosa</i>	1	0.04	1	N/A
small Asian mongoose	<i>Herpestes javanicus</i>	1	0.04	1	N/A

when separated by more than 20 minutes (Yasuda, 2004; Phan & Gray, 2010).

Habitat preferences/activity patterns and effects of human activity. – The Relative Abundance Index for each species with \geq nine encounters was calculated at each camera-trap location with a minimum of 25 trap nights ($n=36$). Differences in mean RAI between camera-traps located in DDF ($n=27$) and SEGF ($n=9$) forest were tested using independent sample t-tests or, when data was non-normally distributed, Mann-Whitney U tests. The effect of human disturbance upon camera trap encounter rates was tested by comparing RAI for each species between camera trap locations within an easy day's walk from villages on the edge of the wildlife sanctuary (i.e. <11 km; $n=18$) with those further away ($n=18$). The correlation between RAI at each camera-trap site (for all species combined) and straight-line distance from village (km) was also examined. Distance to nearest village was used as an easily quantifiable measure of human activity and, in our experience and that of ex-hunter guides, directly correlates with human activity levels. All geographical analysis was conducted in ArcGIS 3.2 (ESRI, 1999).

The use of a simple Relative Abundance Index (RAI) based on camera-trap encounter rates for ecological studies is controversial particularly when comparing between species as a large number of variables (e.g. body size, average group-size, behaviour) are likely to affect trapping rates and detection probability and thus confound the relationship with

actual abundance (Carbone et al., 2001; Jennelle et al., 2002; Treves et al., 2010). However, there is increasing evidence for a linear relationship between RAI and abundance estimated through more rigorous methodologies (Rovero & Marshall, 2009). Therefore, taking into account the caveats above, comparison of RAI of single species among fixed camera-trap locations within our study area is appropriate.

Activity patterns for all species with ≥ 9 encounters were calculated based upon the time imprinted on each photograph. Time periods were pooled to 1-hour intervals with percentage activity level used to calculate whether species were nocturnal ($>90\%$ of encounters 1800–0600 hours), diurnal ($>90\%$ of encounters 0600–1800 hours) or cathemeral (neither prescriptively nocturnal nor diurnal but irregularly active at any time of night or day; van Schaik & Griffiths, 1996; Grassman et al., 2006). For all species we tested if deviations from 10% or 90% were significant (two-tailed at $p < 0.05$) based on binomial distribution probability tests with the probability set at either 0.1 or 0.9, depending on which was closest to the observed percentage of the nocturnal period (van Schaik & Griffiths, 1996; Grassman et al., 2006).

RESULTS

Camera-traps were operational for 2717 camera-trap nights producing a total of 707 independent encounters of 23 species (Table 1). Previously unrecorded species were encountered

less frequently after approximately 750 camera-trap nights with 18 species (78%) recorded after 500 trap-nights and 20 (87%) after 1000 trap-nights (Fig. 2). A total of 11 IUCN-listed species (3 Endangered, 5 Vulnerable and 3 Near Threatened) were recorded (Table 1; Fig. 3).

Red muntjac and Eurasian wild pig were the most frequently recorded species (RAI 6.7 and 5.7 respectively) representing 48% of all encounters. The globally endangered Asian elephant was the third most frequently encountered species, recorded from 55% of camera-traps (Fig. 3). Two species of wild cattle, banteng (the fourth most frequently encountered species) and gaur were recorded (Fig. 3). The carnivore community was represented by 3 cats [the leopard cat, the leopard (Fig. 3) and the clouded leopard] two Canidae (the dhole and golden jackal) and 6 small carnivores (Viverridae/ Mustelidae/ Herpestidae) of which the large Indian civet (RAI 1.66) and the common palm civet (RAI 0.85) were the most frequently encountered. Two primate species, pig-tailed and long-tailed macaques were recorded.

Habitat preferences. – Of the 12 species with sufficient encounters for analysis (Table 1) two, the gaur and pig-tailed macaque, had significantly higher RAI in SEGF than DDF ($z = -1.65$ & -2.75 ; $p = 0.05$ & 0.01 ; Mann-Whitney U test). No species showed significant preference for DDF although the dhole, banteng and large Indian civet were encountered more frequently within this habitat type (Fig. 3). Asian elephant, Eurasian wild pig and red muntjac had higher RAI in SEGF though, again, these differences were non-significant (Fig. 4.).

Human activity. – Red muntjac, Eurasian wild pig and the Asian elephant all had higher RAI at camera-trap locations further than a comfortable day's walk from villages. However this difference was only significant for the most frequently encountered species, the red muntjac ($t = -2.13$; $p=0.04$; independent sample t-test). Few other species showed noticeable differences in RAI between locations close and far from villages (Fig. 5). Across all camera-trap locations there was a significant, if rather weak, positive relationship between overall RAI and distance from village (Pearson correlation = 0.33; $p=0.02$).

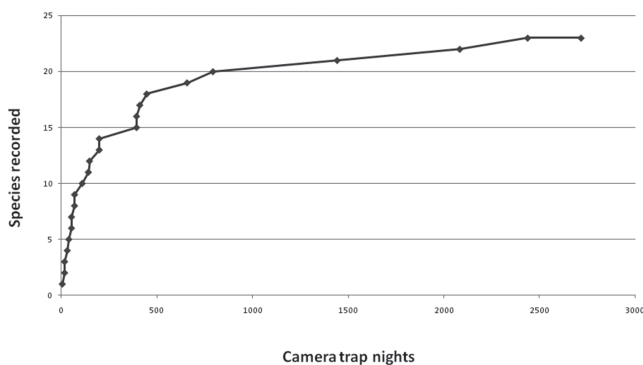


Fig. 2. Increase in species richness (species recorded) with total cumulative number of camera trap nights within Phnom Prich Wildlife Sanctuary (Dec 08–Aug 09).

Activity patterns. – Three species (the east Asian porcupine, large Indian civet and the common palm civet) showed nocturnal activity patterns (Table 1) though this was only significant for the former ($p = 0.04$). All pig-tailed macaque photographs were between 0630–1500 and the species was significantly diurnal ($p < 0.01$). All other species showed cathemeral activity patterns with red muntjac, Eurasian wild pig, Asian elephant, leopard cat and leopard being significantly so ($p = 0.04$ to <0.01 ; Table 1). Although cathemeral, the two most commonly photographed species (red muntjac and

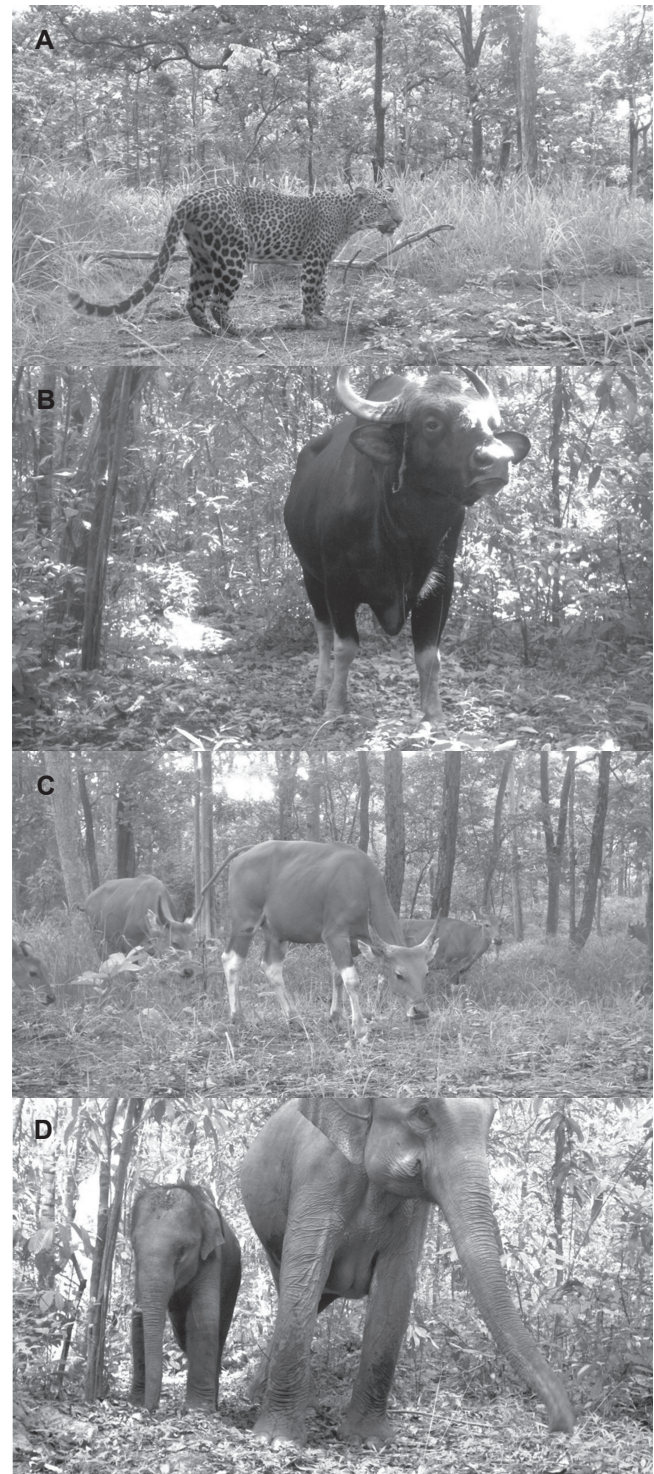


Fig. 3. Camera-trap photographs from Phnom Prich Wildlife Sanctuary: a. leopard; b. gaur; c. banteng; and d. Asian elephant.

Eurasian wild pig) were most active around dawn and dusk, suggesting a degree of crepuscularity (Fig. 6).

DISCUSSION

Our results highlight the global conservation value of the mosaic forests of Phnom Prich Wildlife Sanctuary (PPWS) for terrestrial mammals. Eight globally threatened species were recorded and evidence suggests that this is a fairly intact large mammal community; a rare phenomenon in Indochina. The populations of Asian elephants, the banteng, leopards, dholes and gaurs may be particularly significant given these species' extensive regional declines and the lack of recent records from many Indochinese protected areas (Duckworth & Hedges, 1998; Durbin et al., 2008; Timmins et al., 2008a). On-going research work to estimate robust densities using non-invasive capture-mark-recapture techniques (for the leopard and Asian elephant) and distance-based line transects (wild cattle and other ungulates) can highlight the conservation significance of this landscape for large mammals.

Although the rate of detection of previously unrecorded species began to decline after approximately 750 camera-trap nights, a number of important species believed to be present

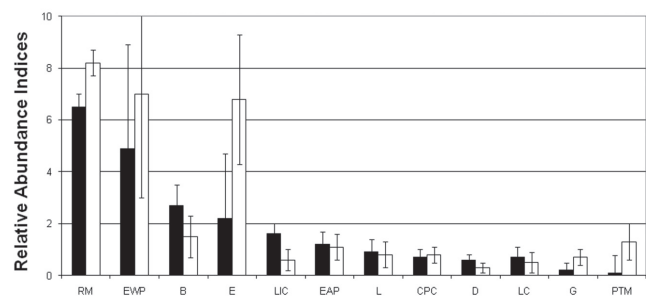


Fig. 4. Mean Relative Abundance Indices (\pm SEM) for 12 most frequently encountered mammal species in PPWS at camera trap locations in DDF (black bars) and SEGf (open bars). RM red muntjac; EWP Eurasian wild pig; B banteng; E Asian elephant; LIC large Indian civet; EAP east Asian porcupine; L leopard; CPC common palm civet; D dhole; LC leopard cat; G gaur; and PTM pig-tailed macaque.

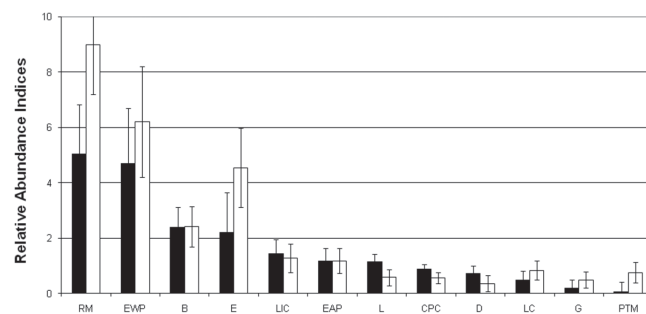


Fig. 5. Mean Relative Abundance Index (\pm SEM) for 12 most frequently encountered mammal species in PPWS at camera trap locations closer (black bars) and further (open bars) than 11-km from nearest village. RM red muntjac; EWP Eurasian wild pig; B banteng; E Asian elephant; LIC large Indian civet; EAP east Asian porcupine; L leopard; CPC common palm civet; D dhole; LC leopard cat; G gaur; and PTM pig-tailed macaque.

within the wildlife sanctuary (e.g. the tiger, *Panthera tigris*; the jungle cat, *Felis chaus*; sambar, *Cervus unicolor*; and the southern serow, *Naemorhedus sumatraensis*) were not encountered. This highlights the fact that camera-trapping studies in which traps are placed to target specific species (in our case large cats and wild cattle) are unlikely to completely inventory the medium-large terrestrial mammal community. Our surveys were also spatially limited to the east of PPWS with much of the protected area not surveyed due to a high risk of camera-trap theft. Whilst capture-recapture statistical techniques exist for modelling species richness and generating expected species accumulation curves (Gotelli & Colwell, 2001; Tobler et al., 2008) in studies such as ours, with camera-trap placement targeting a sub-set of the mammal community, many species are inherently unlikely to be photographed due to behaviour, territoriality, size and specific habitat preferences (Cheyne et al., 2010). Therefore extrapolating overall mammalian species richness across PPWS from our data is unlikely to be meaningful.

Terrestrial mammal habitat preferences in Phnom Prich Wildlife Sanctuary.

– The habitat mosaic of semi-evergreen and mixed-deciduous forests (SEGF) within the wider dominant deciduous dipterocarp forest (DDF) has been recognised as a global conservation priority within the Lower Mekong Dry Forest Ecoregion (Tordoff et al., 2005). Our results provide further evidence for the importance of this mosaic in contributing to the conservation value of PPWS. The majority of terrestrial mammal species recorded were photographed in both habitat types with only two, the gaur and the pig-tailed macaque, showing significant preference for a single forest type. It is likely that the combination of SEGF and DDF provides complementary and critical resources essential for the terrestrial mammal community. The latter, particularly during the wet-season, is likely to be more resource rich, particularly for foragers and their predators. In contrast the denser, less disturbed, SEGF forest provides essential shelter and water, particularly during the hot dry-season, and may also act as important source populations for species more easily hunted and trapped in DDF (Duckworth et al., 2005). The higher encounter rate for the commonest herbivores (red muntjac and Eurasian wild pig) in the denser SEGF forest supports the idea that these refuges from human hunting, and perhaps even natural predation, are important.

More specialist species, that are less able to find refuge in SEGF forest, may be more highly threatened due to hunting

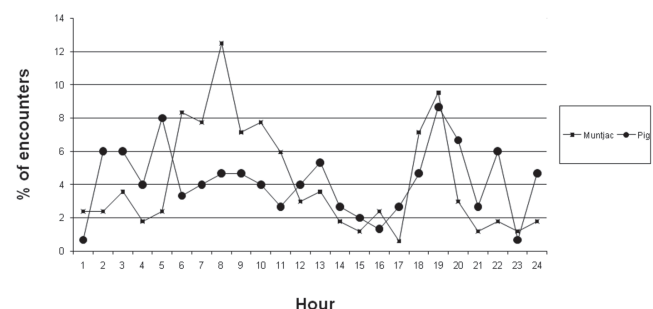


Fig.6. Activity patterns, % of all encounters within each hour, of red muntjacs and Eurasian wild pigs from camera-traps in PPWS.

Table 2. Proportions of nocturnal (1800–0600) activity and sample size of independent photo-encounters, in parentheses, for the red muntjac, Eurasian wild pig, Asian elephant, leopard and gaur based on published camera-trap studies in South-east Asia. ¹This study; ²Azad (2006); ³van Schaik & Griffiths (1996); ⁴Grassman et al. (2006); ⁵Kitamura et al. (2010).

Common Name	East Cambodia ¹	Peninsula Malaysia ²	West Java ³	North Sumatra ³	Central Thailand ⁴	South Thailand ⁵
red muntjac	39% (183)	31% (172)	20% (69)	72% (112)	23% (74)	18% (396)
Eurasian wild pig	57% (155)	16% (774)	11% (302)	42% (24)	26% (38)	18% (426)
Asian elephant	69% (84)	N/A	N/A	50% (8)	54% (37)	N/A
leopard	47% (20)	29% (151)	34% (118)	N/A	N/A	N/A
gaur	75% (8)	N/A	N/A	N/A	63% (35)	N/A

pressure. This lack of potential source populations to replenish heavily hunted DDF areas has been highlighted as a potential reason for the decline of the jungle cat and green peafowl (*Pavo muticus*) within Indochina (Duckworth et al., 2005; Brickle et al., 2008). Both species are DDF specialists and may not be able recover from high hunting pressure in the open forest. Given the much higher encounter rates of dholes in dry forest, this globally endangered species may be highly vulnerable to persecution. As with the jungle cat, few populations exist in Indochina away from the extensive dry forest of northern and eastern Cambodia and the species should be regarded as a conservation priority (Durbin et al., 2008).

The globally threatened gaur showed significantly higher encounter rates in SEGF. While there have been few studies on the ecology or natural history of wild cattle in mainland South-east Asia (Steinmetz, 2004; Pedrono et al., 2009; Phan & Gray, 2010) this study supports the generally held assumption that this species prefers denser, wetter forest than the region's other wild cattle (Wharton, 1957; Steinmetz, 2004). Two globally threatened species, the clouded leopard (VU) and the white-winged wood duck (*Cairina scutulata*) (EN), were also photographed on single occasions within semi-evergreen forest. Given recent work has also highlighted the importance of semi-evergreen forest patches >15 km² in PPWS for the globally endangered yellow-cheeked crested gibbon (*Nomascus gabriellae*) (Gray et al., 2010) these findings highlight the importance of semi-evergreen forest for threatened species within the Lower Mekong Dry Forest Ecoregion.

Effects of human activity on mammal activity patterns within Phnom Prich Wildlife Sanctuary. – While the small sample size of encounters may have precluded detecting significant relationships for all but the most frequently encountered species (i.e. red muntjac) human activity and disturbance seems to be affecting the distribution and activity patterns of terrestrial mammals within PPWS. This likely reflects more intense hunting pressure, both opportunistic using cross-bows and sling shots and more targeting snaring, closer to villages. The three most frequently photographed species (red muntjac, Eurasian wild pig and Asian elephant) all had lower RAI at camera trap locations close to villages. The former two species are, together with the siamese hare and red junglefowl (*Gallus gallus*), the favoured quarry species for both local consumption and the wild meat trade (pers. obs.). Although globally widespread and considered

rather resilient to hunting pressure red muntjac numbers have declined considerably in Indochina and, if restricted to east of the Mekong, would probably merit listing as globally threatened (Timmins et al., 2008b). Throughout Indochina low prey densities are a major contributor to depressing populations of large carnivores (Johnson et al., 2006) and our results indicate that within PPWS numbers of key ungulates may be depressed closer to villages.

While neither wild cattle species showed noticeable difference in encounter rates between camera trap locations close and far from villages it is notable that a considerable proportion of the encounters of both species were at night (75 and 89% of encounters were made between 1800–0600 hours). Similarly in a more extensive analysis of banteng camera-trap photographs from PPWS and the adjacent Monduliri Protected Forest (160 independent encounters) 83% were between 1800–0600 hours (Phan & Gray, 2010). In contrast Halder (1976, in Timmins et al., 2008a) suggested that banteng in Java 'display a more or less fixed diurnal pattern of behaviour' with Hoogerwerf (1970, in Timmins et al., 2008a) also suggesting, again in Java, that banteng 'do not differentiate much in their activities between day and night'. Similarly of 173 camera-trap encounters with the banteng in Ujong Kulon National Park, western Java, only 44% were at night (van Schaik & Griffiths, 1996). The banteng activity patterns documented in this study and Phan & Gray (2010) differ markedly from this. Given that eastern Cambodia experienced extensive hunting from the 1970s until the mid 1990s, and banteng meat remains available in Monduliri with regular confiscations by law enforcement staff (WWF-internal data), it seems likely that the nocturnal patterns of activity we have noted are, at least in part, in response to human activity. Similar variation in the extent of nocturnal behaviour in response to spatial variation in human activity has been detected, through camera-trapping studies, in a number of other hunted species (Griffiths & van Schaik, 1993; Bitetti et al., 2008). It is also notable that whilst the majority of species we photographed showed cathemeral activity patterns we report a higher proportion of nocturnal encounters than from similar studies elsewhere in South-east Asia (Table 2). We suggest this reflects higher incidences of poaching and human disturbance within PPWS than in other South-east Asian protected areas.

Conclusions. – To maintain viable populations of threatened mammal species within PPWS, and to encourage the recovery of populations of flagship carnivores such as the tiger,

strong protected area management is critical. The majority of human activities within the camera-trap study area in eastern PPWS relate to the harvesting of Non-Timber Forest Products (NTFP), primarily *Dipterocarpus alatus* resin and *Strychnos nux-vomica* seeds, and fishing. However these forest-users are often accompanied by domestic dogs and hunt opportunistically for trade and subsistence. Managing and monitoring the activities of NTFP collectors, including banning dogs from protected areas and identifying inviolate core areas, is therefore essential. Given increasing human populations and immigration into villages adjacent to the protected area the intensity of NTFP collection is likely to increase. Therefore respecting protected area boundaries and finalising and enforcing zoning within PPWS is a key component of future management. Such activities are necessary to maintain the conservation integrity of PPWS which, as we have documented, remains high for a suite of globally threatened terrestrial mammal species dependant on the mosaic of forest types.

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