Chapter 9
Density and Activity Patterns of the Globally Significant Large Herbivore Populations of Cambodia's Eastern Plains Landscape

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Abstract The northern and eastern plains of Cambodia support the largest extent of lowland deciduous forest remaining in Southeast Asia. This landscape has also been identified as the highest priority site for tiger *Panthera tigris* recovery in Indochina. We estimated ungulate tiger prey densities using distance-based line transect sampling from two protected areas in the Eastern Plains Landscape between 2009 and 2011. Densities for large ungulates ranged from 1.1 ± SE 0.2 individuals/km^2 for banteng *Bos javanicus* to 2.2 ± SE 0.2 individuals km^2 for red muntjac *Muntiacus muntjak*. The ungulate activity patterns were correlated with activity patterns of extant large carnivores in the landscape with leopard *Panthera pardus* and dhole *Cuon alpinus* showing substantial activity pattern overlap with wild pig *Sus scrofa* and red muntjac, respectively. Overall tiger prey biomass was more than 540 kg/km^2 of which the endangered banteng comprised greater than 80 %. However, ungulate densities were much lower than in ecologically similar sites in South Asia. This was mainly due to the absence of large deer species like *Cervus* deer, which have historically been extensively hunted. Nevertheless, the Eastern Plains landscape likely supports 50–60 % of the global banteng population and remains a high priority area for the conservation of large herbivores in Southeast Asia.

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F.S. Ahrestani and M. Sankaran (eds.), *The Ecology of Large Herbivores in South and Southeast Asia*, Ecological Studies 225,
DOI 10.1007/978-94-017-7570-0_9

Keywords Banteng · Cambodia · Distance-based line transect sampling · Tiger prey

9.1 Introduction

The northern and eastern Cambodian provinces of Mondulkiri, Ratanakiri, Stung Treng, and Preah Vihear support some of the largest extents of lowland deciduous forest in Southeast Asia (Todorff et al. 2005). These forests had once been described as one of the "great game-lands of the world; a Serengeti of Asia" and had historically supported a diverse and abundant megafaunal assemblage of ungulates, predators and scavengers (Wharton 1957; Todorff et al. 2005). The ungulate component included at one time an assemblage of four sympatric wild cattle species (gaur *Bos gaurus*, banteng *Bos javanicus*, kouprey *Bos sauvelli* and wild water buffalo *Bubalus arnee*); a unique distinction as few regions in the world have supported more than two sympatric wild cattle species.

The Eastern Plains Landscape (EPL), Mondulkiri province, in eastern Cambodia (Fig. 9.1) forms part of the Lower Mekong Dry Forest Ecoregion (Olson and Dinerstein 1998; Tordoff et al. 2005). This landscape of rolling lowlands, generally under 150 m asl, is characterized by extensive deciduous dipterocarp forest, including open grassland areas (*veal*) with a high frequency fire regime, and smaller patches of mixed deciduous and semi-evergreen forests on higher ground and along watercourses. The EPL deciduous forest is bisected by a number of rivers including one major tributary of the Mekong, the Srepok River, and is studded with small seasonal wetlands (*trapeang*).

The wider landscape in which the EPL is situated suffered considerable political instability and conflict throughout the latter half of the 20th century, which intensified during the Lon Nol (1970–75) and Pol Pot (1975–79) regimes, and persisted into the late 1990s. During this time there was evidence of large declines in the population and distribution of large mammal species including tiger *Panthera tigris*, leopard *P. pardus*, Asian elephant *Elephas maximus*, banteng, gaur and Eld's deer *Cervus eldii* (Loucks et al. 2008). These declines were associated with a proliferation of firearms, the development of an external market for wildlife products and, particularly during the Khmer Rouge era, government sponsored hunting (Loucks et al. 2008). This hunting pressure led to the global extinction of one large herbivore species endemic to Indochina, the kouprey (Timmins et al. 2008a, b; Timmins 2011), and more recently the extinction of the tiger from the landscape due to targeted poaching of the remaining individuals (Gray et al. 2012a; O'Kelly et al. 2012).

Almost four–fifths of the EPL (13,730 km^2) lie within protected areas; four wildlife sanctuaries managed by the General Department for Administration of

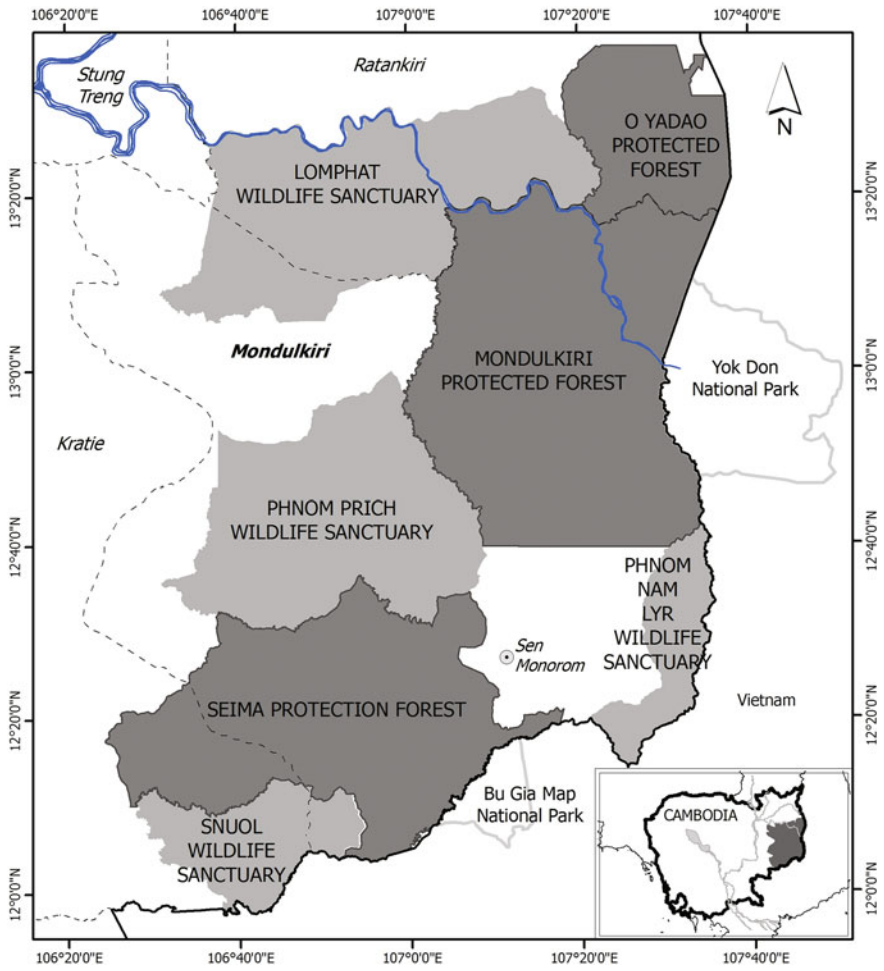

Fig. 9.1 Protected areas within the Eastern Plains Landscape Cambodia and Vietnam

Nature Conservation and Protection of the Ministry of Environment, and three protection forests managed by the Forestry Administration of the Ministry of Agriculture, Forestry and Fisheries (Table 9.1). Furthermore, two areas in Vietnam adjacent to the EPL are gazetted as national parks; Bu Gia Map (12.7°N 107.1°E; 260 km^2), South of Seima Protection Forest, and Yok Don (12.5°N 107.4°E; 1,155 km^2), the largest national park in Vietnam, to the east of Mondulkiri Protected Forest (13.0°N 107.3°E). With improved security resulting from a stable political climate the EPL region has, since the early 2000s, been the focus of conservation activity by government conservation departments supported by

Table 9.1 Protected areas of the Eastern Plains Landscape province with government management authorities (Forestry Administration [FA], Ministry of Environment [MoE]), and supporting nonovernmental organisations (Wildlife Conservation Society [WCS], World Wide Fund for Nature [WWF].

Protected area	Management	Area (km^2)	Elevation range (m)	Forest cover (%)		
				DDF	MDF	SEGF/EGF
Seima Protection Forest [SPF]	FA and WCS	2,990	70–650	42	15	31
Mondulkiri Protected Forest [MPF]	FA and WWF	3,730	120–450	82	9	1
Phnom Prich Wildlife Sanctuary [PPWS]	MoE and WWF	2,200	100–640	69	23	5
Lumphat Wildlife Sanctuary [LWS]	MoE and BirdLife	2,510	100–260	78	6	6
Snoul Wildlife Sanctuary	MoE	750	70–130	3	8	65
Phnom Nam Lyr Wildlife Sanctuary	MoE	540	320–1070	28	16	44
O'Yadao Protected Forest	FA	1,010	100–320	72	14	7

Forest cover estimated from JICA (2006); percentages exclude non-forest areas. DDF deciduous dipterocarp forest; MDF mixed deciduous forest; SEGF/EGF semi-evergreen, and evergreen forest

international nongovernmental organisations. Since 2002, the World Wide Fund for Nature (WWF) Greater Mekong Program has assisted the Royal Cambodian Government with protected area management activities within two protected areas in the Eastern Plains Landscape: Mondulkiri Protected Forest (MPF) and Phnom Prich Wildlife Sanctuary (PPWS) (Fig. 9.1). These protected areas have received approximately $9,000,000 in international conservation investment during this period. This investment has supported protected area infrastructure development, the recruitment and training of ranger enforcement patrols, biological monitoring, improved judiciary response, and alternative livelihood work with communities adjacent to the protected area.

Mondulkiri Protected Forest (MPF) and Phnom Prich Wildlife Sanctuary (PPWS) cover approximately 7,000 km^2 in the heart of the Eastern Plains Landscape and comprise a mosaic of deciduous dipterocarp, mixed deciduous, and semi-evergreen forest (Table 9.1). The two protected areas support at least 19 critically endangered or endangered mammal, bird, and reptile species (Table 9.2). Since 2008 we have been studying large herbivore and predator communities within the core areas of MPF and PPWS (Phan and Gray 2010; Gray and Phan 2011; Gray and Prum 2012; Gray 2012; Gray et al. 2012b, 2013; Gray et al. 2014), largely though distance-based line transect sampling and camera trapping.

Table 9.2 Critically endangered (CR) and endangered (EN) species of mammal, bird, and reptile recorded from Phnom Prich Wildlife Sanctuary (PPWS) and Mondulkiri Protected Forest (MPF) and the conservation significance of the landscape population

Species		IUCN	PPWS	MPF	Significance
Wild Water Buffalo	*Bubalus arnee*	CR			Global?
Tiger	*Panthera tigris*	CR			Regional?
Silvered Langur	*Trachypithecus germaini*	EN			Global
Black-shanked Douc	*Pygathrix nigripes*	EN			Global
Yellow-cheeked Crested Gibbon	*Nomascus gabriellae*	EN			Global
Eld's Deer	*Cervus eldii*	EN			Global
Banteng	*Bos javanicus*	EN			Global
Dhole	*Cuon alpinus*	EN			Regional
Asian Elephant	*Elephas maximus*	EN			Regional
White-rumped Vulture	*Gyps bengalensis*	CR			Global
Slender-billed Vulture	*Gyps. tenuirostris*	CR			Global
Red-headed Vulture	*Sarcogyps calvus*	CR			Global
Giant Ibis	*Pseudibis gigantea*	CR			Global
White-shouldered Ibis	*Pseudibis davisoni*	CR			Global
Green Peafowl	*Pavo munticus*	EN			Global
White-winged Duck	*Cairina scutulata*	EN		??	Regional
Masked Finfoot	*Heliopais personata*	EN			Regional?
Siamese Crocodile	*Crocodylus siamensis*	CR			Global
Elongated Tortoise	*Indotestudo elongata*	EN			Regional?

Shaded cells indicate confirmed presence in each of the protected areas

9.2 Large Herbivore Densities and Their Conservation Significance in Cambodia's Deciduous Dipterocarp Forests

We surveyed 110 line transects that were 1–4 km long and randomly distributed within the 3,400 km^2 core areas of Mondulkiri Protected Forest and Phnom Prich Wildlife Sanctuary during the dry seasons of 2009/10 and 2010/11. Surveys followed the protocols of Karanth and Nichols (2002) for line transect sampling of large herbivores. Total survey effort was 1,310 km resulting in 325 encounters with large herbivores (Table 9.3). We used the conventional distance sampling (CDS) engine in software DISTANCE 6.0 (Thomas et al. 2010) to estimate densities following the protocols of Thomas et al. (2010). Despite the extensive survey effort the numbers of encounters of three large ungulate species (gaur, sambar *Cervus unicolor*, and Eld's deer) were too low for density estimation.

Table 9.3 Number of encounters, mean (and range) cluster size, and encounter rates (encounters per 10 km surveyed) of large ungulates during line transect surveys in Mondulkiri Protected Forest and Phnom Prich Wildlife Sanctuary in 2010 and 2011

Species	Number of encounters	Cluster size	Encounter rate (encounters/10 km)
Gaur	3	1.7 (1–3)	0.02
Banteng	63	4.7 (1–16)	0.48
Sambar	5	1.2 (1–2)	0.04
Eld's Deer	2	2 (1–3)	0.02
Red Muntjac	198	1.1 (1–4)	1.51
Wild Pig	54	4.7 (1–25)	0.41

Species with sufficient observations for density estimation are highlighted

Table 9.4 Sample size of observations used in models (N), densities per km^2(± SEM), 95 % confidence interval range of density estimates and associated population size (number of individuals) (± SEM) and 95 % confidence interval range of population size for Banteng, Red Muntjac, and Wild Pig in the core areas of Mondulkiri Protected Forest and Phnom Prich Wildlife Sanctuary based on estimates from distance-based line-transect sampling

Species	N	Density km^{-2} ± SE	Density % CV	Density 95 % CI range	Population size ± SE	Population size 95 % CI range
Banteng	51	1.1 ± 0.2	19	0.8–1.7	3920 ± 750	2700–5690
Red muntjac	182	2.2 ± 0.2	10	1.8–2.6	7400 ± 750	6060–9030
Wild pig	48	1.4 ± 0.4	25	0.9–2.3	4900 ± 1220	3040–7970

Eastern Plains Landscape wide densities for large ungulates ranged from 1.1 ± SE 0.2 individuals/km^2 for banteng to 2.2 ± SE 0.2 individuals/km^2 for red muntjac *Muntiacus muntjak* (Table 9.4). Using estimated species weights from Karanth and Sunquist (1992), the densities suggest a prey biomass of approximately 540 kg/km^2, of which banteng comprise more than 80 %. Estimated population sizes of species across the entire study area were 2700–5700 banteng, 6000–9000 red muntjac, and 3000–8000 wild pig *Sus scrofa* (Table 9.4).

As far as we are aware the only other site with similarly robust estimates for ungulates in Indochina (sensu Laos, Cambodia, and Vietnam) is the adjacent Seima Protected Forest. In 2010 density estimates, from the 1,800 km^2 core area of Seima, based on a 1,600 km survey effort of 40 transects lines, were 0.29 wild cattle (both banteng and gaur)/km^2, 1.8 red muntjac/km^2, 2.0 wild pig/km^2, and 0.1 sambar/km^2 (O'Kelly and Nut 2010). This corresponds to an overall large ungulate density of 4.2 individuals/km^2 providing a biomass of approximately 260 kg/km^2.

A number of other studies have attempted to quantify tiger prey densities and biomass, largely in semi-evergreen and evergreen forests, in Southeast Asia. However, only a few of these studies employed the scientifically robust distance-based line transect sampling methodology that had been used to survey the Eastern Plains Landscape (O'Brien et al. 2003; WCS-Thailand 2008). For example, in the mosaic of semi-evergreen, mixed deciduous, and deciduous dipterocarp forests in Huai Kha Khaeng Wildlife Sanctuary, western Thailand, overall large ungulate

densities are estimated at 6.2 individuals per km^2 (2008 data based on 45+ line transects and 1,000 km+ survey effort; WCS-Thailand 2008). Red muntjac was the most abundant species (2.2 individuals/km^2) followed by sambar (1.9 individuals/km^2) and wild pig (1.6 individuals/km^2). Wild cattle densities were estimated at 0.2 banteng/km^2 and 0.4 gaur/km^2 (WCS-Thailand 2008). Steinmetz and Mather (1996) estimated *Muntiacus* spp. density in semi-evergreen and mixed deciduous forest in Thung Yai Naresuan Wildlife Sanctuary, western Thailand, to be 1–2 individuals/km^2 based on 360 km of line transect sampling.

Large ungulate density estimates have also been published from lowland rainforest in Bukit Barisan National Park, Sumatra where sambar density was 0.6–1.4 individuals/km^2, red muntjac 1.8–4.4 individuals/km^2, and wild pig 4.4–6.0 individuals/km^2 (O'Brien et al. 2003). Srikosamatara (1993) estimated densities and biomass of wild cattle, sambar, and red muntjac from Huai Kha Khaeng Wildlife Sanctuary based on distance sampling of droppings from line transects calibrated against defecation and decomposition rates. Density estimates were approximately 1.8 wild cattle/km^2, 1.9–4.2 sambar/km^2, and 3.1 red muntjac/km^2 giving an overall biomass of 1,250 kg/km^2. By extrapolating of camera-trap encounter rates, Kawanishi and Sunquist (2004) estimated densities of wild pig (3.4–4.6 individuals/km^2) and red muntjac (3.2–4.1 individuals/km^2), which provided a biomass of 200–400 kg/km^2 of tiger prey species in Taman Negara, peninsular Malaysia. Using the Royle-Nichols occupancy heterogeneity model, Vongkhamheng (2011) estimated an ungulate density of 5.3 individuals/km^2 (primarily *Muntiacus* spp. and wild pig with a few sambar) in largely evergreen forest in Nam Et-Phou Louey NPA, northern Laos. However, calculating abundance from such occupancy models based on sign-encounter rates is dependent upon a large number of assumptions and is unlikely to be as robust, or accurate, as estimates generated from distance-based line transect sampling. In contrast to the paucity of reliable data from South–East Asia, there is, however, a wealth of robust data on large ungulate densities from South Asia, where published densities, based on distance-based line transect sampling, in protected areas range from 7 (Wang 2010) to 250+ individuals per km^2 (Wegge and Storaas 2000) with 50+ individual ungulates per km^2 being the norm in most Indian tiger reserves (Karanth and Nichols 2000). The EPL estimate of <5 individuals per km^2 is clearly at the low end of the ungulate density spectrum for deciduous dipterocarp forests; for example, in ecologically similar lowland sal deciduous forest in Ranthambore Tiger Reserve ungulate density is approximately 75 animals/km^2 (Bagchi et al. 2003). Despite this disparity densities of smaller ungulates (red muntjac and wild pig) within the Eastern Plains Landscape are similar to many South and Southeast Asian protected areas (Table 9.5). Steinmetz et al. (2010) found that in areas with minimal hunting in western Thailand, muntjac densities were generally 1–3 individuals/km^2.

Although wild pig have been recorded to reach densities of 40+ individuals per km^2 following mass seeding of dipterocarps in lowland evergreen dipterocarp forest in peninsular Malaysia (Ickes 2001), densities of 1–4 individuals/km^2 are typical throughout the species' cosmopolitan world range (Melis et al. 2006). Although O'Kelly and Nut (2010) suggested red muntjac and wild pig densities are lower in

Table 9.5 Densities of selected large ungulates from distance-based line transect surveys from South and South–East Asian Tiger landscape

Location	<45 kg		>45 kg	
	Red muntjac	Wild pig	Sambar	Chital
Bardia, Nepal[a]	1.5	1.5	n/a	267.0
Rajaji, India[b]	n/a	1.9	14.6	49.9
Pench, India[c]	n/a	n/a	9.6	51.3
Nagarahole, India[d]	4.2		50.6	5.5
Ranthambhore, India[e]	n/a	9.8	17.2	31.0
Kanha, India[c]	0.6	n/a	1.5	49.7
Bandipur, India[c]	0.7	n/a	5.6	20.1
Bhadra, India[f]	3.6	n/a	0.9	4.5
Jigme, Bhutan[g]	2.2	3.7	1.2	n/a
South Asian mean	***2.1***	***4.2***	***12.7***	***59.9***
Huai Kha Khaeng, Thailand[h]	2.2	1.6	1.9	n/a
Bukit Barisan, Indonesia[i]	1.8–4.4	4.4–6.0	0.6–1.4	n/a
PPWS-MPF, Cambodia[j]	2.2	1.4	n/a	n/a
SPF, Cambodia[k]	1.8	2.0	0.1	n/a
South–East Asian mean	***2.3***	***2.6***	***1***	

Data sources [a] Wegge and Storaas (2000); [b] Harihar et al. (2008); [c] Karanth and Nichols (2000); [d] Karanth and Sunquist (1992); [e] Bagchi et al. (2003); [f] Jathana et al. (2003); [g] Wang (2010); [h] WCS-Thailand (2008); [i] O'Brien et al. (2003); [j] This study; [k] O'Kelly and Nut (2010)

Seima Protected Forest than would be expected in sites without hunting, we believe that populations of red muntjac and wild pig are relatively healthy across the Eastern Plains Landscape. Although there was evidence that both species were still being hunted in all protected areas surveyed, the density estimates of both species from the Eastern Plains Landscape were similar to those from ecologically similar protected areas in South and Southeast Asia (Table 9.5), suggesting that both species may be fairly resilient to current levels of hunting pressure in the landscape.

The shortfall in prey densities within the Eastern Plains Landscape in comparison with ecologically similar sites in South Asia and Southeast Asia appears to be mainly due to the low abundances of larger (>45 kg) deer species, like sambar and Eld's deer (Table 9.5). This is worrying as large cervids make up more than three-quarters of prey consumed by tiger across most of its range (Karanth and Nichols 2002). The reasons for the low densities of sambar and Eld's deer in the Eastern Plains are unclear, but similar patterns of low densities and slow recoveries of *Cervus* deer, even when other ungulate species are increasing, have been noted elsewhere in Southeast Asia. For example, in Thung Yai Wildlife Sanctuary, western Thailand, Steinmetz et al. (2010) suggested that the sambar's mating system, in which females select for prime males, made the sambar less resilient to

recovery following hunting when compared to other ungulates (such as red muntjac, wild pig and gaur) when prime sambar males had been selectively targeted as hunting trophies. Similarly Aung et al. (2001), from a radio tracking study of Eld's deer in deciduous dipterocarp forest in Myanmar, suggested that the species' social organization and life history traits differed from other tropical cervids. Eld deer showed tightly synchronized seasonal breeding and low reproductive output by females, which could contribute to low levels of population recovery following hunting. Given the importance of large cervids in tiger diets, additional research into natural history and the role of behavior in these species' recovery patterns is essential.

9.3 Significance of Banteng Population

The Eastern Plains Landscape supports two globally endangered large ungulates: banteng and Eld's deer. While we obtained insufficient observations for density estimation of Eld's deer, our data, also published in Gray et al. (2012b), provides the first robust density and population estimate of banteng from anywhere within the species' global range. This suggests that Mondulkiri Protected Forest and Phnom Prich Wildlife Sanctuary support the majority of the global population of banteng, and that previous estimates of the species' Cambodian and global population sizes are low. The IUCN Red List suggests the global population of banteng is '*unlikely to be more than 8,000 and is quite possibly fewer than 5,000 animals… no subpopulation is believed to exceed 500 individuals and only 6–8 subpopulations of more than 50 animals, are known'* (Timmins et al. 2008a, 2008b). If our estimate of 2,700–5,700 banteng (with a mean of 3,900 individuals) in Mondulkiri Protected Forest and Phnom Prich Wildlife Sanctuary is accurate, then the IUCN information would need to be substantially revised. This study and that of O'Kelly and Nut (2010) in the adjacent Siema Proteced Forest, which suggested a population 100–700 (mean 250) individuals in Siema, are the only banteng population estimates we could find to be derived from robust sampling methodologies accounting for imperfect detection. A review of our data indicates that the assumptions of distance sampling were largely met, and therefore we strongly believe that there is little reason to doubt the accuracy of our estimates. Indeed, the majority of sampling errors which are likely to affect distance sampling of large ungulates, for example evasive movement away from transect lines prior to detection and failing to observe all individuals in groups, will lead to underestimating rather than overestimating density (Wegge and Storaas 2000).

Assessing the global significance of the banteng population in the Eastern Plains Landscape is hindered by the lack of any accurate, scientific population estimates from elsewhere in the species' range. Table 9.6 summarizes the species' status from

Table 9.6 Banteng population estimates from range states

Range State (subspecies)	Population size	Data source
B. j. javanicus		
Java, Indonesia	700–1300	Pudyatmoko (2004)
B. j. lowi		
Kallimantan, Indonesia	? < 50?	IUCN-red list
Sabah, Malaysia	?300–500?	IUCN-red list
B. j. birmanicus		
Myanmar	?<500?	Estimate
Laos	?<50?	Estimate
Vietnam	74–103	Pedrono et al. (2009)
Thailand	470	Srikosamatara and Suteethorn (1995)
MPF-PPWS-SPF	2800–6400	This study and O' Kelly and Nut (2010)
Cambodia-rest	?1000–1500?	Estimate

Estimates are marked with? not based on published sources

other range countries, though numbers for Myanmar, Laos, Borneo, and the remainder of Cambodia are essentially optimistic estimates of maximum populations based on limited fieldwork. A better global population estimate, therefore, might be 5,600–11,000 individuals, though there is great uncertainty in the population estimates besides those from the Eastern Plains Landscape. We strongly recommend robust surveying for Banteng elsewhere in the species' range, particularly at sites such as Huai Kha Khaeng Wildlife Sanctuary, Thailand (estimated population 290 individuals; Srikosamatara and Suteethorn 1995), and Ujong Kulon (estimated population 300–800 individuals; Pudyatmoko 2004) and Baluran (estimated population 206 individuals; Pudyatmoko 2004) National Parks, Java, where distance-based line transect surveys appear practical. As in our study areas it is possible that these may result in substantial upwards revisions of known population estimates.

Considering the maximum possible population sizes elsewhere in the species' range, the protected area complex of Mondulkiri Protected Forest-Phnom Prich Wildlife Sanctuary-Siema Protected Forest supports 50–60 % (upper and lower 95 % confidence intervals respectively) of the global banteng population (Table 9.6). These protected areas are therefore clearly the global stronghold and are irreplaceable for the conservation of this enigmatic and beautiful species. Given the presence of banteng in at least three other protected areas in eastern Cambodia (Lumphat Wildlife Sanctuary and O'Yadao Protected Forest) and adjacent Vietnam (Yok Don National Park—population estimate 30–44 individuals; Pedrono et al. 2009), it is possible that the banteng population in EPL may be even higher than our estimates. However hunting, for wild meat and trophy horns, remains a major threat in these protected areas where enforcement levels are much lower than in our study areas.

9.4 Large Herbivore Activity Patterns and Interactions with Carnivores

Understanding the control that extant large predator populations exert on large herbivore populations is important for conservation management focussed at reviving populations of both threatened large herbivores and their predators. The deciduous dipterocarp forests of the Eastern Plains Landscape, similar to much of tropical Asia, historically supported two *Panthera* species (tiger and leopard) together with dhole *Cuon alpinus* and a suite of smaller cat species (Gray et al. 2014). Where the three species co-occur today, inter-specific competition appears to affect behavior, movement patterns , and prey selection, particularly where large ungulate prey densities are reduced (Stoen and Wegge 1996; Karanth and Sunquist 2000; Odden et al. 2010). The tiger, however, is most likely extinct in the landscape (O'Kelly et al. 2012), but the leopard remains relatively abundant with an estimated density of 3.8 (±SE 1.9) individuals/100 km^2 (Gray and Prum 2012), which is comparable with estimates in well protected national parks in Thailand.

We wanted to test, like foraging theory suggests, if whether carnivores synchronize their activity patterns with those of their principal prey species to optimize foraging behavior (Stephens and Krebs 1987; Linkie and Ridout 2011). We, therefore, deployed 50 camera-trap pairs (Reconyx RapidFire Professional PC90; Reconyx, Inc., Holmen, WI) within approximately 210 km^2 of the core area of Mondulkiri Protected Forest during the late dry season (March–July 2009) for a total of 3,711 camera-trap pair nights (mean 77.5 per location). Camera-traps were located either side of routes (i.e., motorbike trails, dry-river beds, and ridgelines) designed to maximize encounters with large carnivores (for more details of camera-trap study design see Gray and Prum 2012). All independent encounters (defined as successive photographs separated by >20 min; Phan et al. 2010) of leopard, dhole, and large herbivores were recorded.

Overlap between the activity patterns of leopard, dhole, and the two most frequently photographed large herbivores (red muntjac and wild pig) were assessed using a statistical model developed by Ridout and Linkie (2009). The Ridout and Linke (2009) model calculates probability density functions of each species' activity pattern using kernel density estimates (Taylor 2008). Overlap between the density distributions of any two species is estimated using the coefficient of overlapping Δ_4 (Weitzman 1970), which ranges from 0 (no overlap) to 1 (complete overlap; Ridout and Linkie 2009). Linkie and Ridout (2011) suggested that $\Delta_4 > 0.8$ indicated strongly overlapping activity patterns.

The range of independent encounters of the four target species captured by the camera-traps was between 33 (dhole) and 442 (red muntjac) (Table 9.7). Although active throughout the day and night (i.e., cathemeral activity pattern), leopard displayed clear crepuscular activity with 26 % of encounters between 0401–0659 h and 19 % between 1701–1959 h. Dhole were predominantly diurnal (Table 9.7), and wild pig and red muntjac were cathemeral with encounters throughout the 24-h cycle. However, wild pig was distinctly more nocturnal than red muntjac

Table 9.7 Number of independent encounters (sensu Phan et al. 2010), and proportion of nocturnal (i.e., 18h01–05h59) encounters, of leopard, dhole, red muntjac, and Eurasian wild pig, during camera-trapping in Mondulkiri Protected Forest, March–June 2009

Species	# independent encounters	# (%) of nocturnal (18h01–05h59) encounters
Leopard	141	81 (57)
Dhole	33	4 (12)
Red muntjac	442	96 (21)
Wild pig	307	158 (51)

(Table 9.7); red muntjac activity peaked after dawn with 36 % of encounters between 0601–0859 h. The activity pattern of leopard overlapped with wild pig more than it did with red muntjac, while the activity pattern of dhole overlapped more with red muntjac than it did with wild pig (Figs. 9.2 and 9.3).

The close temporal overlap between the daily activities of leopard and wild pig, and between dhole and red muntjac suggest that there may be specialization in prey selection by the two large carnivores in Mondulkiri Protected Forest. Although considered a generalist predator, a detailed meta-analysis found that leopard preferentially prey on ungulate species that have a body mass of 10–40 kg and occur in small herds in dense forest habitats (Hayward et al. 2006). However, inter-specific competition with tiger may result in leopard targeting suboptimal prey, for example langurs *Semnopithecus* spp., particularly when ungulate densities are reduced (Ramakrishnan et al. 1999; Karanth and Sunquist 2000; Steinmetz et al. 2013). In sites such as Mondulkiri Protected Forest, where tigers are absent, wild pig may be an ideal prey for leopard given their relative abundance (approximate density 1.9 individuals per km^2), optimal body mass (~38 kg; Karanth and Sunquist 1992), and their herding behavior.

Dhole preferentially prey upon medium to large cervids in South Asia, particularly chital and sambar, and it has been suggested that the primarily diurnal activity patterns of the dhole reflects those of its prey (Karanth and Sunquist 2000;

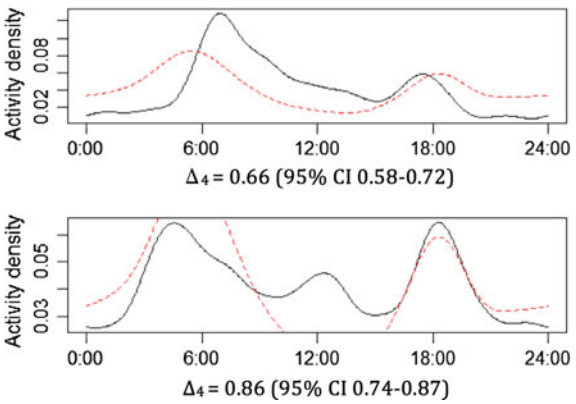

Fig. 9.2 Activity overlap between leopard and red muntjac (*top*), and leopard and wild pig (*below*) based on camera-trapping in Mondulkiri Protected Forest, Cambodia. Δ_4, a measure of activity overlap, was calculated based on Linkie and Ridout (2011); $\Delta_4 > 0.8$ indicates strongly overlapping activity patterns

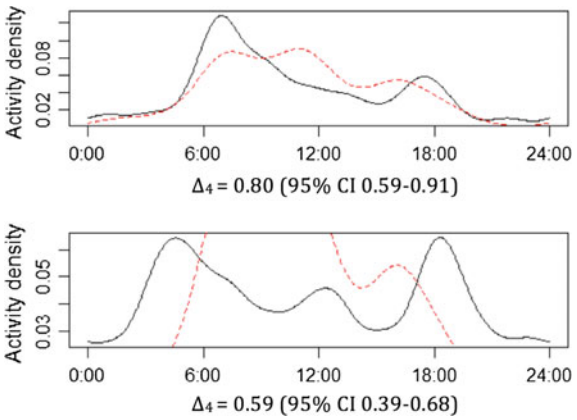

Fig. 9.3 Activity overlap between dhole and red muntjac (*top*) and dhole and wild pig (*below*) based on camera-trapping in Mondulkiri Protected Forest, Cambodia. Δ_4, a measure of activity overlap, was calculated based on Linkie and Ridout (2011); $\Delta_4 > 0.8$ indicates strongly overlapping activity patterns

Andheria et al. 2007; Borah et al. 2009). However, in tropical Southeast Asia, where ungulate densities are reduced, muntjac spp., and even mouse-deer *Tragulus* spp., predominate in dhole scat analysis (Grassman et al. 2005; Kawanishi and Sunquist 2008; Kamler et al. 2012; Steinmetz et al. 2013). The strong temporal overlap found in this study between the activity patterns of the muntjac and dhole in Mondulkiri Protected Forest provides further support for the importance of muntjac in dhole diets in Southeast Asia. Sambar, which dominates dhole diet in other sites, occurs at very low densities in Mondulkiri Protected Forest (4 camera-trap encounters during this study) probably due to hunting pressure. Recovery of sambar populations, therefore, appears to be important for large carnivore conservation in Mondulkiri Protected Forest. Diet studies, involving scat analysis, are recommended for further understanding carnivore–prey interactions in eastern Cambodia.

9.5 Conclusions

The data that our co-workers and us have presented over the past 6 years (Phan and Gray 2010; Gray and Phan 2011; Clements et al. 2012; Gray 2012; Gray and Prum 2012; Gray et al. 2012b; O'Kelly et al. 2012; Wright et al. 2012; Gray et al. 2013) have confirmed the global significance of Mondulkiri Protected Forest, Seima Protection Forest, and Phnom Prich Wildlife Sanctuary for biodiversity conservation. This particularly applies for the long-term conservation of large herbivores in the Southeast Asian region. The documented banteng population is substantially higher than previously estimated and is likely to represent >50 % of the global population of this endangered species. However overall large ungulate densities, <5 individuals per km^2, are much lower than the intrinsic carrying capacity of deciduous dipterocarp forest. This appears to be largely due to the scarcity of large deer (sambar and Eld's deer).

The landscape goals of WWF Greater Mekong are to recover large ungulate, and thus tiger and other carnivore populations. However, for this to happen, stronger protected area management and a commitment to conservation from the highest levels in the Cambodian government are necessary. All protected areas within the EPL are severely threatened by social and agricultural land concessions and infrastructure projects. While red muntjac and wild pig may be resilient to current levels of hunting and the high population of banteng is encouraging, the low densities of *Cervus* deer, the high potential for the banteng population to decline, and the high levels of widespread poaching and hunting are major causes for concern. All these factors would need to be addressed for the EPL to be once again the 'Serengeti of Asia'.

Acknowledgments This study forms part of WWF Greater Mekong Cambodia Country Program's Eastern Plains Landscape Project. Major funding comes from WWF-US, WWF-Sweden, WWF-Germany, and Humanscale. Work in Mondulkiri Protected Forest is with permission of the Forestry Administration of the Ministry of Agriculture Forestry and Fisheries with support from His Excellency Cheng Kimsun, Men Phymean, Song Keang, and Keo Sopheak. Work in Phnom Prich Wildlife Sanctuary is with permission of the Ministry of the Environment and support from His Excellency Chay Samith, Sanrangdy Vicheth, and Han Sakhan. This project would not have been possible without the hard work and dedication of our field teams: Khaev Oudom, Ing Seangnirithy, Lien Nor, and Van Sonny (MPF) and Sary Tre, Sin Somoan, Se Noun, and Chan Touy (PPWS). Craig Bruce, Pin Chanrattanak, Nick Cox, Keith Metzner, Amy Malling, Pem Maly, Michelle Owen, and Seng Teak provided logistical and administrative support whilst Hannah O'Kelly, Bivash Pandav, Abishek Harihar, Paul Doggerty, Shannon Barber-Meyer, and Barney Long assisted in study design, survey objectives, and provided statistical advice.

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