# ACTIVITY PATTERNS AND HOME RANGES OF INDOCHINESE LEOPARD PANTHERA PARDUS DELACOURI IN THE EASTERN PLAINS LANDSCAPE, CAMBODIA

# Thomas Neill Edward Gray<sup>1</sup>

#### ABSTRACT

Indochinese Leopard Panthera pardus delacouri is amongst the most poorly known Leopard subspecies with few studies on its natural history. I undertook camera-trapping in the core area of Mondulkiri Protected Forest, eastern Cambodia, to examine Leopard activity patterns and home-ranges based on camera-trap encounters with uniquely marked individuals. Understanding Leopard ecology in the protected area is essential given plans to reintroduce Tiger Panthera tigris to the landscape. A total of 50 camera-trap pairs, operational for 3,711 camera-trap pair nights, produced 142 independent encounters with 12 individually identifiable Leopards. Encounters of female Leopards with cubs demonstrated reproduction within the protected area. Minimum convex polygon use-areas of four male Leopards captured more than ten times were between 10 and 93 km<sup>2</sup> and covered the entire 210-km<sup>2</sup> camera-trapping grid with minimal overlap between individuals. Although methods are not directly comparable, this is larger than previously published Leopard home-range estimates in Asia. Combined with Leopard densities lower than in ecologically similar protected areas in South Asia, this suggests that depressed prey densities are limiting the Leopard population. Leopard activity patterns were correlated with those of Red Muntjac Muntiacus muntjak and Wild Pig Sus scrofa. Additional Leopard research in the landscape featuring diet studies, radio or GPS collaring, and long-term monitoring within a capture-mark-recapture framework, is recommended.

Key Words: camera-trapping, large carnivore, deciduous dipterocarp forest, home range, Indochina.

## INTRODUCTION

Leopard (*Panthera pardus*) is globally near-threatened and, while the most-studied *Panthera* species, little is known of the ecology or status of Southeast Asian populations (WEBER & RABINOWITZ, 1996; UPHYRKINA *ET AL.*, 2001). Within Indochina (*sensu* Cambodia, Laos and Vietnam) Leopard populations (considered to be a subspecies, *Panthera pardus delacouri*) have undergone massive declines due to a combination of poaching, habitat loss, and prey depletion, and the species is now largely restricted to a few protected areas (DUCKWORTH & HEDGES, 1998). Historically Leopard co-occurred with Tiger (*P. tigris*) throughout its Asian distribution and there is evidence that inter-specific competition affects Leopard behaviour, movement patterns, and prey selection in the presence of Tiger (KARANTH & SUNQUIST, 2000; AHMED & KHAN, 2008; ODDEN *ET AL.*, 2010, NGOPRASERT *ET AL.*,

<sup>&</sup>lt;sup>1</sup> WWF Greater Mekong Cambodia Country Program, Eastern Plains Landscape Project, Phum Doh Kromum, Sen Monorom, Cambodia. E-mail: tomnegray@hotmail.com Received 1 November 2012; accepted 28 May 2013.

2012; STEINMETZ *ET AL.*, 2013). However, across vast areas of the species' ancestral range, Tiger is no longer present and Leopard may be the dominant large carnivore. Given the global commitment to prevent Tiger extinction, and plans to repopulate former Tiger areas, understanding Leopard ecology and densities is critical (SEIDENSTICKER, 2010). For example, recent evidence from the Terai Arc of India has demonstrated how Leopard distribution, abundance, and diet has changed following Tiger recovery, leading to increased human-wildlife conflict (HARIHAR *ET AL.*, 2011). I report on Indochinese Leopard natural history based on camera-trapping in the core of Mondulkiri Protected Forest, a protected area within the Eastern Plains Landscape of eastern Cambodia. The landscape is dominated by deciduous dipterocarp forest and Tiger appear ecologically extinct (LYNAM, 2010; O'KELLY *ET AL.*, 2012). The aims of the study were to examine use-areas and spatial patterns of Leopard distribution based on camera-trap encounters with uniquely marked individual Leopards. I also compare previously published estimates of leopard density from Mondulkiri Protected Forest (GRAY & PRUM, 2012) with other sites in Southeast and South Asia to assess Leopard density within a regional context.

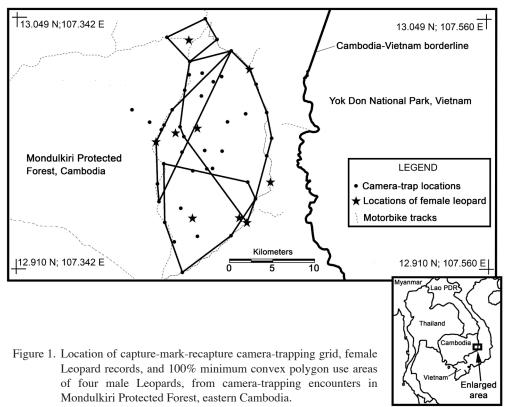
# STUDY AREA

Mondulkiri Protected Forest (approx. location 13.10N; 107.40E) is located in eastern Cambodia and forms part of the Eastern Plains Landscape, a protected area complex of over 13,000 km<sup>2</sup> including Yok Don National Park in Dak Lak province, Vietnam (Fig. 1). The core area of Mondulkiri Protected Forest is approximately 1,500 km<sup>2</sup> and consists of a matrix of dominant flatland deciduous dipterocarp forest with smaller patches of semi-evergreen and mixed deciduous forest. Biodiversity surveys have revealed Mondulkiri Protected Forest is globally significant for conservation with recent records of Wild Water Buffalo (*Bubalas arnee*), Banteng (*Bos javanicus*), Siamese Crocodile (*Crocodylus siamensis*), Giant Ibis (*Pseudibis gigantea*) and White-shouldered Ibis (*P. davisoni*) (PHAN *ET AL.*, 2010; GRAY *ET AL.*, 2012). Despite extremely low numbers, LYNAM (2010) considered the Eastern Plains Landscape irreplaceable for Indochinese Tiger (*P. t. corbetti*) conservation, representing the only large block of dry forest habitat in Southeast Asia, and recommended a reintroduction program. Distance-based line transect sampling has documented large (>15-kg) ungulate densities of between 5 and 7 individuals per km<sup>2</sup> in the core area of Mondulkiri Protected Forest (GRAY *ET AL.*, 2013).

## METHODS

## **Camera-Trapping**

Intensive camera-trapping was undertaken within approximately 210 km<sup>2</sup> of the core area of Mondulkiri Protected Forest; located south of the Srepok River and between 2 and 20 km west of the Vietnam border (Fig. 1). Camera-trap pairs were deployed in a grid pattern following the protocols of NICHOLS & KARANTH (2002) for closed population capture-recapture studies on large carnivores. Fifty camera-trap (Reconyx RapidFire Professional PC90; Reconyx, Inc., Holmen, WI) pairs were located either side of routes (i.e., motorbike



Mainland Southeast Asia

trails, dry riverbeds, and ridgelines) designed to maximize encounters with large carnivores. Cameras were spaced approximately 2–3 km apart thereby ensuring that no individuals had a non-zero capture probability (i.e. camera-trap spacing sufficiently small to ensure no home-ranges between cameras). All camera-trap images were digitally stamped with the date and time of capture. Camera-traps were operational between 18 March and 30 June 2009 for a total of 3,711 camera-trap-pair nights (mean 77.5 per location).

## Data Analysis

All Leopard photographs were extracted from the camera-trap data and camera-trap location and date and time of capture were recorded. Individual Leopards were identified based on unique pelage patterns. Previously published analysis of Leopard encounters from this data set estimated a density of 3.8 ( $\pm$  SE 1.9) individuals per 100 km<sup>2</sup> using the Chao heterogeneity estimator and the half mean maximum distance moved (HMMDM) buffer (GRAY & PRUM, 2012).

Activity patterns of Leopard were calculated based upon the time imprinted on each photograph with the time-of-day of encounters in camera-traps assumed to correlate with activity levels. Time periods were pooled to one-hour intervals for analysis. Daily (24-hour) movement patterns of individual Leopards were assessed by identifying all occasions

when individual Leopards were photographed more than once within a 24-hour period from different camera-trap locations, and calculating straight-line distances moved. For all individual Leopards with more than ten encounters, 100% Minimum Convex Polygon (MCP) use-areas were plotted. These represented the minimum area individual Leopards used during the course of the study period.

# RESULTS

## **Leopard Encounters**

Camera-trapping produced a total of 142 independent (defined as successive photographs separated by >20 minutes; PHAN *ET AL.*, 2010) Leopard encounters with between 1 and 24 (mean 3.3) photographs per encounter (total 470 photographs). In 95 encounters (67%) the Leopard photographed could be identified to an individual based on unique pelage patterns. A total of 12 individual Leopards (5 males and 7 females) were identified and these were encountered between 1 and 44 times each (mean 7.9 ± SD 12.5; Table 1).

All but four encounters were with single individuals. Female D was encountered once accompanied by two cubs (<25% the size of the adult). When this individual was subsequently photographed four weeks later, 2.2 km from the original location, the cubs were not detected. On three additional occasions two Leopards were photographed together, with one individual approximately three-quarters the size of the other. This occurred twice on the same night (approximately 90 minutes and 2.3 km apart) and subsequently 20 days later 3.5 km to the south. Unfortunately the quality of the photographs prevented these individuals being identified and it is unclear whether they represent the same two individuals, presumably a mother and large cub.

Leopard ID	Sex	Number of captures	Number of locations	Number of dates	100% MCP home range size (km <sup>2</sup> )
А	Female	2	1	2	n/a
В	Male	16	7	14	27
С	Male	44	11	27	93
D	Male	11	5	9	10
Е	Female	2	2	2	n/a
F	Female	2	2	2	n/a
G	Female	1	1	1	n/a
Н	Female	1	1	1	n/a
Ι	Male	12	7	9	59
J	Male	2	2	2	n/a
Κ	Female	1	1	1	n/a
L	Female	1	1	1	n/a

Table 1. Individual Leopards photographed by camera-traps in Mondulkiri Protected Forest March to May 2009.

Although active throughout the day and night (i.e. cathemeral activity pattern) Leopard displayed clear crepuscular activity within the study area with 26% of encounters between 04h01 and 06h59 and 19% between 17h01 and 19h59 (Fig. 2). Leopard activity patterns largely appeared to mirror those of Red Muntjac (Muntiacus muntjak) and Wild Pig (Sus *scrofa*) (Figure 2; Red Muntjac n = 444 and Wild Pig n = 307; data from independent cameratrap encounters during this study). 100% MCP use-areas of the four individuals (Males B, C, D and I) with more than 10 encounters each were between 10 and 93 km<sup>2</sup> (mean 47 km<sup>2</sup>; Table 1). The use-areas were largely non-overlapping and covered the 211-km<sup>2</sup> study area (Fig. 1). All four use-areas were bordered by the edge of the camera-trapping grid and were therefore constrained by the location of camera-traps. It is therefore likely that all individuals were also using areas outside the camera-trapping grid and that the use areas represented the minimum areas utilised during the sampling period. All but one of the ten female encounters were within the MCP use-areas of the four males (Fig. 1). On 22 occasions the same individual Leopard was photographed from different camera-trap locations within a 24-hour period. Mean distances moved during 12-hour periods were 5.2 km during the night and 5.5 km during the day. Within a 24-hour period the mean distance moved by the same individual Leopard was 7.5 km (range 5-8.6 km).

#### DISCUSSION

Indochinese Leopard is amongst the least well known subspecies of Leopard with little published data on natural history, densities, or population size. Although camera-trapping

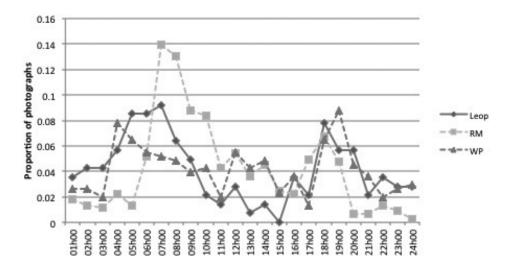


Figure 2. Activity patterns, derived from proportion of independent photographic encounters per hour, for Leopard (Leop), Red Muntjac (RM), and Wild Pig (WP) from camera-trapping in Mondulkiri Protected Forest, eastern Cambodia.

is widely used to monitor Tiger in South and Southeast Asia (e.g. KARANTH *ET AL.*, 2004; SIMCHAROEN *ET AL.*, 2007; RAYAN & MOHAMMAD 2009) there appear to be few published estimates of Leopard density from the region based on robust capture-mark-recapture analysis (Table 2). Whilst the estimate of  $3.8 \pm \text{SE} 1.9$  individuals per 100 km<sup>2</sup> of GRAY & PRUM (2012) in Mondulkiri Protected Forest is lower than that reported from Indian Tiger reserves it is similar to estimates from semi-evergreen and mixed deciduous forest in the Western Forest Complex of Thailand (Table 2).

Data from this study on Leopard use-areas and movement patterns is clearly constrained by the locations of camera-traps, and therefore represent minimum values, with all useareas bounded by the edge of the camera-trapping grid. However given the extremely limited published data on Leopard ecology and natural history in Southeast Asia I believe this information is valuable. Published Leopard home-range estimates in Asia, based on radio-telemetry, range between approximately 20 and 50 km<sup>2</sup> using 95% Minimum Convex Polygon estimates (GRASSMAN, 1999; KARANTH & SUNQUIST, 2000; ODDEN & WEGGE, 2005; SIMCHAROEN *ET AL.*, 2008). Although this method removes outliers from the data, and is thus not directly comparable with information from this study, the recorded 100% Minimum Convex Polygon use-area of Male C, greater than 90 km<sup>2</sup>, is larger than any of these published estimates. Year-round radio telemetry or GPS-collar studies are recommended to better understand Leopard home-range size and movements within Mondulkiri Protected Forest.

The spatial distribution of use-areas I report, with minimal overlap between the use areas of different males, strongly matches published studies on Leopard territory spacing in Asia (e.g. GRASSMAN, 1999; ODDEN & WEGGE, 2005) and Africa (e.g. MIZUTANI & JEWELL, 1998; MARKER & DICKMAN, 2005). The mean recorded distance moved by males per day,

Study area	Leopard density (individuals per 100 km <sup>2</sup> ( $\pm$ SE)	Reference
Sariska Tiger Reserve, India	23.15 ± (8.12)	Chauhan <i>et al.</i> , 2005
Mudumalai Tiger Reserve, India	13.4 (± 2.7) – 28.4 (± 7.2)	Kalle et al., 2011
Rajaji National Park, India	14.99 (±6.9)	HARIHAR <i>et al.</i> , 2009
Kaeng Krachan National Park, Thailand	4.8 (± 2.7)	Ngoprasert, 2004
Kuiburi National Park, Thailand	3.3 ( $\pm$ 2.4) and 4.8 ( $\pm$ 2.8)	STEINMETZ ET AL., 2009
Mondulkiri Protected Forest, Cambodia	3.8 (± 1.9)	Gray & Prum, 2012
Jigme Singye Wangchuck National Park, Bhutan	1.04 (± 0.01)	Wang & MacDonald, 2009

Table 2. Published Leopard densities based on capture-mark-recapture of camera-trap data from protected areas in South and Southeast Asia.

although clearly constrained by location of camera-traps, is also similar to published studies from across the species' range (e.g. MARKER & DICHMAN, 2005; ODDEN & WEGGE, 2005). Previous camera-trapping studies in Southeast Asia also report similar activity patterns as in this study with Leopard generally cathemeral but with activity peaks around dawn and dusk (AZAD, 2006; NGOPRASERT *ET AL.*, 2007; GRAY & PHAN, 2011). However in areas with Tiger presence, such as Kuiburi National Park Thailand, there is some evidence that Leopard are mainly diurnal (STEINMETZ *ET AL.*, 2013).

The reason for the relatively low density and large home-range size of Leopard in Mondulkiri Protected Forest when compared with ecologically similar areas of Asia is unclear but may be a result of depressed prey populations. Several authors have described an inverse relationship between food availability and territory size in territorial animals (e.g. SCHOENER, 1981; SAITOH, 1991). Whether Leopard territories in the Eastern Plains Landscape of Cambodia are larger than in other Asian protected areas as a result of reduced prey densities merits further research. The majority of protected areas in South Asia have prey densities orders of magnitude higher than in eastern Cambodia and, based on the limited published data, Leopard home-ranges are smaller than recorded in this study. For example, in Bardia National Park, Nepal: ungulate density >100 individuals km<sup>-2</sup>; mean male Leopard home range 47 km<sup>2</sup> (ODDEN & WEGGE 2005); Nagerhole Tiger Reserve, India: ungulate density 75 individuals km<sup>-2</sup>, mean male Leopard home range size 28.2 km<sup>2</sup> (KARANTH & SUNQUIST 2000).

Ungulate densities in the core area of Mondulkiri Protected Forest are clearly substantially lower than the carrying capacity of deciduous dipterocarp forests as inferred from ungulate densities within ecologically similar deciduous forests of South Asia (GRAY ET AL., 2013). However, this appears largely due to the rarity of large deer (e.g. Cervus/ Axis) (GRAY ET AL., 2013) which may not be important Leopard prey. Studies in Thailand, in sites where Tiger also occur, have demonstrated that Leopard is a generalist predator with Hog Badger (Arctonyx collaris) the predominant prey species in Huai Kha Khaeng Wildlife Sanctuary (GRASSMAN, 1999) and Presbytis/Trachypithecus langurs in Kuiburi National Park (R. Steinmetz in litt., 2013). Both Hog Badger and *Trachypithecus* langurs are rare within the deciduous dipterocarp forests of eastern Cambodia (pers. obs.). In Mondulkiri Protected Forest Leopard activity patterns correlate with those of the most abundant ungulates in the landscape, Red Muntjac and Wild Pig, suggesting these may be important prey species. This matches conclusions from predictive models of Leopard occurrence across 13 protected areas in Thailand, based on camera-trap data, which indicated Leopards were associated with habitats where Red Muntjac and Wild Pig were most likely to be present (NGOPRASERT ET AL. 2012). Densities of these species are at similar levels to those reported in South Asian protected areas (GRAY ET AL., 2013). It is therefore unclear the extent to which ungulate availability affects Leopard density and home-range size in the Eastern Plains Landscape. Prey selection studies in Mondulkiri Protected Forest, based on analysis of Leopard scat, are therefore clearly warranted.

In addition to possible prey depletion hunting may also be limiting Leopard densities. In August 2010, 8 kg of Leopard bones and a single fresh Leopard skin, originating from a Leopard recently snared in the Mondulkiri Protected Forest buffer zone, were confiscated by Mondulkiri Protected Forest law enforcement teams (R. Singh in litt., 2013). Strong law enforcement is clearly required to ensure both large carnivore and prey recovery within the landscape.

## ACKNOWLEDGEMENTS

This study was conducted as part of WWF Greater Mekong Cambodia Program's Eastern Plains Landscape project. Project funding was provided by WWF-US, WWF-Sweden and Human Scale. Work in Mondulkiri Protected Forest is in collaboration with the Forestry Administration of the Ministry of Forestry Fisheries and Agriculture, Cambodia and we thank His Excellency Chheng Kim Soun, Men Phymean, Keo Omaliss and Keo Sopheak for support. Prum Sovanna, Lien Kha, Lien Nor, Mel Track, Me Camphoung, Phan Channa and Khaev Oudom assisted in camera-trapping. Two anonymous reviewers and George Gale provided valuable comments to an earlier version of this manuscript and Craig Bruce, Barney Long, Bivash Pandav, and Seng Teak assisted in project planning and logistics.

#### REFERENCES

- AHMED, K., AND J. KHAN. 2008. Food habits of leopard in tropical moist deciduous forest of Dudhwa National Park, Uttar Pradesh, India. Int. J. Ecol. Env. Sci. 34: 141–147.
- AZAD, M. A.J.B. A. G, 2006. Mammal diversity and conservation in a secondary forest in Peninsular Malaysia. Biod. Cons. 15: 1013–1025.
- CHAUHAN, D. S., A. HARIHAR, S. P. GOYAL, Q. QURESHI, P. LAL, AND V. B. MATHUR. 2005. Estimating leopard population using camera traps in Sariska Tiger Reserve. Wildlife Institute of India, Dehradun, India.
- DUCKWORTH, J. W., AND S. HEDGES. 1998. Tracking Tigers: A review of the status of Tiger, Asian elephant, gaur and banteng in Vietnam, Lao, Cambodia and Yunnan (China). WWF Indochina, Hanoi, Vietnam.
- GRASSMAN, L. I. 1999: Ecology and behaviour of the Indochinese leopard in Kaeng Krachan National Park, Thailand. Nat. Hist. Bull. Siam Soc. 47: 77–93.
- GRAY, T. N. E., AND C. PHAN. 2011. Habitat preferences and activity patterns of the larger mammal community in Phnom Prich Wildlife Sanctuary, Cambodia. *Raffles Bull. Zool.* 59: 311–318.
- GRAY, T. N. E., AND S. PRUM. 2012. Leopard density in a post-conflict landscape Cambodia: evidence from spatially explicit capture-recapture. J. Wild. Manage. doi: 10.1002/jwmg.230.
- GRAY, T. N. E., R. OU, K. HUY, C. PIN, AND A. L. MAXWELL. 2012. The status of large mammals in eastern Cambodia: a review of camera-trapping data 1999–2007. *Cambodian J. Nat. Hist.* 4: 42–55.
- GRAY, T. N. E., C. PHAN, C. PIN, AND S. PRUM. 2013. Establishing a monitoring baseline for threatened large ungulates in eastern Cambodia. Wild. Biol. 18: 406–413.
- HARIHAR, A., B. PANDAV, AND S. P. GOYAL. 2009. Density of leopards (*Panthera pardus*) in the Chilla Range of Rajaji National Park, Uttarakhand, India. *Mammalia* 74: 83–87.
- HARIHAR, A., B. PANDAAV, AND S. P. GOYAL. 2011. Response of leopard Panthera pardus to the recovery of a tiger Panthera tigris population. J. Appl. Ecol. 48: 806–814.
- KALLE, R., T. RAMESH., Q. QURESHI, AND K. SANKAR. 2011. Density of tiger and leopard in a tropical deciduous forest of Mudumalai Tiger Reserve, southern India, as estimated using photographic capture–recapture sampling. *Acta Theriologica* doi: 10.1007/s13364-011-0038-9
- KARANTH, K. U., AND M. E. SUNQUIST. 2000. Behavioral correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. J. Zool. 250: 255–265.
- KARANTH, K. U., R. S. CHUNDAWAT, J. D. NICHOLS, AND N. S. KUMAR. 2004. Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. *Anim. Cons.* 7: 285–290.
- LYNAM, A. 2010. Securing a future for wild Indochinese tigers: transforming tiger vacuums into tiger source sites. Integr. Zool. 5: 324–334
- MARKER, L. L., AND A. J. DICKMAN. 2005. Factors affecting leopard spatial ecology with particular reference to Namibian farmlands. S. African J. Wildl Res. 35: 105–115.
- MIZUTANI, F., AND P. A. JEWELL. 1998. Home range and movements of leopards (*Panthera pardus*) on a livestock ranch in Kenya. J. Zool. 244: 269–286.
- NGOPRASERT, D. 2004. Effects of roads, selected environmental variables and human disturbance on Asiatic leopard (*Panthera pardus*) in Kaeng Krachan National Park. MSc. Thesis. School of Bioresource and Technology.

King Mongkut's University of Technology Thonburi, Bangkok, Thailand.

- NGOPRASET, D., A. J. LYNAM, AND G. A. GALE. 2007. Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx* 41: 343–351.
- NGOPRASERT, D., A. J. LYNAM, R. SUKMASUANG, N. TANTIPISANUH, W. CHUTIPONG, R. STEINMETZ, K. E. JENKS, G. A. GALE, L. I. GRASSMAN, S. KITAMURA, J. HOWARD, P. CUTTER, P. CUTTER, P. LEIMGRUBER, N. SONGSASEN, AND D. H. REED. 2012. Occurrence of three felids across a network of protected areas in Thailand: prey, intraguild, and habitat associations. *Biotropica* 44: 810–817.
- NICHOLS, J. D., AND K. U. KARANTH. 2002. Statistical concepts: estimating absolute densities of tigers using capturerecapture sampling. In: (K. U. Karanth and J. D. Nichols, eds.) A manual for researchers, managers and conservationists in tropical Asia. Centre for Wildlife Studies, Bangalore, India. pp 124–137.
- O'KELLY, H. J., T. D. EVANS, E. J STOKE, T.J. CLEMENTS, D. AN, M. GATELY, M. NUT, E. H. B. POLLARD, S. MEN, AND J. WALSTON. 2012. Identifying conservation successes, failures and future opportunities; assessing recovery potential of wild ungulates and tiger in eastern Cambodia. *PLoS ONE* 7(10): e40482. doi:10.1371/journal. pone.0040482
- ODDEN, M., AND P. WEGGE. 2005. Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal. Wildl. Biol. 11: 145–152.
- Odden, M., P. WEGGE, AND T. FREDRIKSEN. 2010. Do tigers displace leopards? If so, why? Ecol. Res. 25: 875-881.
- PHAN, P., S. PRUM, AND T. N. E. GRAY. 2010. Recent camera trap records of globally threatened species from the Eastern Plains Landscape, Mondulkiri. *Cambodian J. Nat. Hist.* 2:89–93.
- RAYAN, D. M., AND S. W. MOHAMMAD. 2009. The importance of selectively logged forests for tiger *Panthera tigris* conservation: a population density estimate in Peninsular Malaysia. *Oryx* 43: 48–51.
- SAITOH, T. 1991. The effects and limits of territoriality on population regulation in grey red-backed voles, *Clethrionomys rufocanus bedfordiae. Res. Pop. Ecol.* 33: 367–386.
- SCHOENER, T. W. 1981. An empirically based estimate of home range. Theor. Pop. Biol. 20: 281-325.
- SEIDENSTICKER, J. 2010. Saving wild tigers: a case study in biodiversity loss and challenges to be met for recovery beyond 2010. Integr. Zool. 5: 285–299.
- SIMCHAROEN, S., A. PATTANVIBOOL, K. U. KARANTH, J. D. NICHOLS, AND N. S. KUMAR N. 2007. How many tigers Panthera tigris are there in Huai Kha Khaeng Wildlife Sanctuary, Thailand? An estimate using photographic capture-recapture sampling. Oryx 41, 447–453.
- SIMCHAROEN, S., A. C. D. BARLOW, A. SIMCHAROEN, AND J. L. D. SMITH. 2008. Home range size and daytime habitat selection of Leopards in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Biol. Cons.* 141: 2242–2250.
- STEINMETZ R., N. SEUATURIEN, W. CHUTIPONG, AND B. POONNIL. 2009. The ecology and conservation of tigers and their prey in Kuiburi National Park, Thailand. WWF Thailand, and Department of National Parks, Wildlife, and Plant Conservation, Bangkok.
- STEINMETZ, R., N. SEUATURIEN, AND W. CHUTIPONG. 2013. Tigers, leopards and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. *Biol. Cons.* (in press).
- UPHYRKINA, O., W. E. JOHNSON, H. QUIGLEY, D. MIQUELLE, L. MARKER, M. BUSH, AND S. J. O'BRIAN. 2001. Phylogenetics, genome diversity and origin of modern leopard, *Panthera pardus. Mol. Ecol.* 10: 2617–2633.
- WANG, S. M., AND D. W. MACDONALD. 2009. The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biol. Cons.* 142: 606-613.
- WEBER, W., AND A. RABINOWITZ. 1996. A global perspective on large carnivore conservation. *Cons. Biol.* 10: 1046–1054.