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Co-existence patterns of large sympatric carnivores as influenced by their habitat use in a tropical deciduous forest of Central India

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Habitat used by tiger, leopard and dhole was assessed between June 2006 and April 2011 in Central India. Indirect evidences (pugmark, scrape, scats) of these three large sympatric carnivores were collected from carnivore sign survey (total effort 1162 km in winter and 1674 km in summer) in each sampling unit [i.e. forest beat (n = 44) of the intensive study area (410 km^2)]. A total of 1303 and 2238 locations of tiger evidence, 362 and 608 locations of leopard evidence and 264 and 324 locations of dhole evidence were recorded in winter and summer, respectively. Significant difference ($p = 0.02$) was found between summer and winter use of habitats by three large carnivores. We pooled data of same seasons across year as there was no significant difference ($p = 0.09$). All locations were plotted on the classified land use and land cover map and Digital Elevation Model maps and percentage of locations in each class was calculated. The utilized habitat locations were compared with randomly generated available habitat locations (n = 1500) for seasonal habitat selection. It was observed that all three carnivores selectively utilized different habitats. Significant seasonal habitat separation was observed between tiger, leopard and dhole while utilizing different land use and land cover types in both winter ($p = 0.0001$) and summer ($p = 0.01$) and terrain types in winter ($p = 0.001$). This may have allowed them to co-exist in the study area. Protection of the habitat in Pench and surrounding areas is crucial for the survival of large carnivores in this landscape.

Key words: Tiger, leopard, dhole, habitat use, spatial separation, Pench.

INTRODUCTION

Habitat loss and fragmentation are the main challenges in conservation and management of large carnivores worldwide (Peyton, 1999). Habitat fragmentation can result in small, isolated populations which become increasingly vulnerable to extinction (Diamond, 1986; Wilcove, 1987). Animals generally select habitats that satisfy their demands for food, water, and denning sites to optimize survival and reproduction (Boyce & McDonald, 1999; Chamberlain *et al.*, 2002). Though, several hypotheses have been proposed to explain the co-existence patterns of large carnivores in forested habitats (Karanth & Sunquist, 1995); a comparison of habitat use by sympatric species allows an assessment of their interactions. Previous studies have indicated that habitat separation is the most common form of niche partitioning in sympatric species of mammals (Brown & Lieberman, 1973). According to Marsh & Harris (2000), habitat separation between closely related species is one of the most common forms of co-existence. Schoener (1974) also considered habitat separation to be responsible for multispecies co-existence. Information on habitat use and habitat separation is thus crucial to understand the relationship between distribution and abundance of wildlife species (Tejeda-Cruz *et al.*, 2009). This information can be helpful to assess not only habitat requirements of animals but also support sound wildlife management plans (Morrison *et al.*, 2006).

In India, tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) were found utiliz-

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ing a wide range of habitats (Johnsingh, 1983; Karanth & Sunquist, 1995; Edgaonkar, 2008; Jhala *et al.*, 2008, 2010). In tropical Asia, tigers inhabit forests of deciduous, evergreen, riverine, swamp and mangrove, showing incredible tolerance to variation in altitude, temperature and rainfall regimes. Leopards too, have the ability to adapt in different habitats and feeding on a variety of prey as well as they have the capacity of surviving in close proximity to humans (Hamilton, 1976). The factors which govern dhole habitats are prey abundance, water availability, interspersion of forests with grassy openings, minimum human disturbance and potential den sites (Johnsingh, 1985; Acharya *et al*., 2007). Conservation of habitat of these sympatric carnivores in the human dominated landscape of India is always been a challenging task for wildlife managers (Wikramanayaeke *et al*., 1998) as their habitats have been fragmented because of various biotic pressure (Qureshi *et al*., 2006; Jhala *et al*., 2008). The reported occupancy of tiger, leopard and dhole in Central Indian landscape in 2006 was 48610 km^2, 117913 km^2 and 85962 km^2, respectively, and 38056 km^2, 92786 km^2 and 71817 km^2, respectively, in 2010 (Jhala *et al*., 2010).

With the decline of most of the large carnivore habitats from the central Indian landscape (Qureshi *et al*., 2006; Jhala *et al*., 2010), there was an urgent need for adopting the effective practical methods to understand the utilization patterns of different habitat resources by tiger, leopard and dhole. Seasonal (winter and summer) utilization of major habitat resources at the population level by each of these species was compared with the available habitat types (Manly *et al.*, 2004) in Pench Tiger Reserve (PTR), Madhya Pradesh. The study area has forest connectivity with PTR, Maharastra and forms one of the most important conservation units for large carnivores in central Indian landscape (Qureshi *et al.*, 2006; Jhala *et al.*, 2010). A detailed long-term study on spatio-temporal utilization of major habitat resources by three co-occurring large carnivores together has not been documented earlier in the central Indian landscape. The objectives of the present study were 1) to evaluate the seasonal utilization of different land use, land cover and terrain types by three large sympatric carnivores and 2) to evaluate the implications of seasonal habitat separation among the three large carnivores for their co-existence in this landscape.

MATERIALS AND METHODS

The study was conducted in Pench Tiger Reserve (PTR), Madhya Pradesh (79° 09′ E to 79° 22′ E and 21° 38 N′ to 21° 50′ N), India. The total geographical area of PTR (758 km^2) consists of Pench National Park (PNP), Pench Wildlife Sanctuary (PWS) and Reserved Forests. Both, PNP and PWS were considered as intensive study area (410 km^2). The terrain is undulating and the elevation ranged between 350 m and 650 m (Sankar *et al*., 2001). There are three distinct periods; summer (March-June), monsoon (July-September) and winter (October-February). Mean annual rainfall was 1400 mm occurring largely in monsoon period. Temperature varies from a minimum of 1°C in winter to 45°C in summer (Sankar *et al*., 2001). Vegetation is broadly classified into tropical dry deciduous and tropical moist deciduous forests (Champion & Seth, 1968). The Pench river, which is the major source of perennial water, is dammed downstream of the study area, leading to the inundation of 54 km^2 area of the National Park. A significant part of study area comes under sub-mergence habitat. The draw down area coming under the submergence of Totladoh reservoir (Pench Hydro-electric project) is 11.7 km^2 and cover 1.55% of PTR (Sankar *et al*., 2001). As summer approaches, these areas, from where the water gradually recedes downstream, become lush green meadows attracting high numbers of wild herbivores. The miscellaneous forest type, more of a moist-deciduous forest and gaps in canopy had lots of grass (Acharya, 1997). This forest type constitutes major association of *Boswellia serrata*, *Anogeissus latifolia*, *Buchanania lanzan*, *Lannea coromandelica*, *Miliusa velutina*, *Bauhinia racemosa* and *Soymida febrifuga* (Dungariyal, 2008). In a teak-mixed forest, more than 75% vegetation type comprised of *Tectona grandis* followed by other species such as *Miliusa velutina*, *Terminalia tomentosa*, *Lagerstroemia parviflora, Bauhinia racemosa*, *Ougeinia oojeinensis*, *Grewia tiliaefolia* and bamboo (*Dendrocalamus strictus*) (Dungariyal, 2008).

Wild ungulates comprised of chital (*Axis axis*), sambar (*Rusa unicolor*), nilgai (*Bosephalus tragocamelus*), gaur (*Bos gaurus*), barking deer (*Muntiacus muntjac*), chousingha (*Tetracerus quadricornis*) and wild pig (*Sus scrofa*). Apart from tiger, leopard and dhole, other carnivore species in PTR are golden jackal (*Canis aureus*) and jungle cat (*Felis chaus*). Primate species found are common langur (*Semnopithecus entellus*) and Rhesus macaque (*Macaca mulatta*) (Biswas & Sankar, 2002). The Indian porcupine (*Hystrix indi-*

ca), black-naped hare (*Lepus nigricollis*), flying fox (*Pteropus giganteus*), flying squirrel (*Petaurista petaurista*), three stripped squirrel (*Funambulus palmarum*) and Indian pangolin (*Manis crassicaudata*) also occur in PTR. No human habitation is found in PTR. There are over 51648 inhabitants in 107 villages around the notified buffer zone of PTR. The locals are predominantly tribal (62%) and mostly depend upon agriculture. However, domestic livestock such as water buffaloes (*Bubalis bubalis*) and cattle (*Bos indicus*) graze along the boundaries of the Reserve (Sankar *et al.*, 2001; Dungariyal, 2008).

Utilisation of different land use, land cover and terrain types

Indirect (pugmark, scrape, fresh scats) evidences of co-occurring carnivores were collected from carnivore sign survey (Jhala *et al.*, 2005) between June 2006 and April 2011. Forest beats were considered as the lowest sampling unit for sign survey and three separate routes of each forest beats were walked early in the morning to record the signs and tracks of these three carnivores. Each search covered about 4 to 6 km distance in areas having the best potential for carnivore presence. In total, 44 beats from intensive study area were covered for data collection and a hand held Global Positioning System (GPS) was used to record all evidences.

All these locations were plotted on the classified land use and land cover map (Fig. 1) and elevation classes or Digital Elevation Model (DEM) map (Fig. 2) of the study area and the habitat variables for each point locations were extracted using program ArcGIS 9.2 (Singh, 2011). Land use and land cover were categorized into six categories: sub-mergence, riverine, miscellaneous, agriculture, barren land and teak mixed forest, whereas terrain or elevation types were categorized as: elevation between 350 m and 500 m and elevation between 501 m and 650 m. Percentage of locations in each land use, land cover and terrain class were calculated as suggested by White & Garrot (1990) and Aebischer *et al.* (1993).

Random points for available habitat resources

To select adequate available point locations for the present study, 500, 1000, 1500, 2000 and 2500 random points were generated within the 100% Minimum Convex Polygon (MCP) using ArcGIS 9.2 (Hosmer & Lemeshow, 2000; Singh, 2011). Fifteen hundred

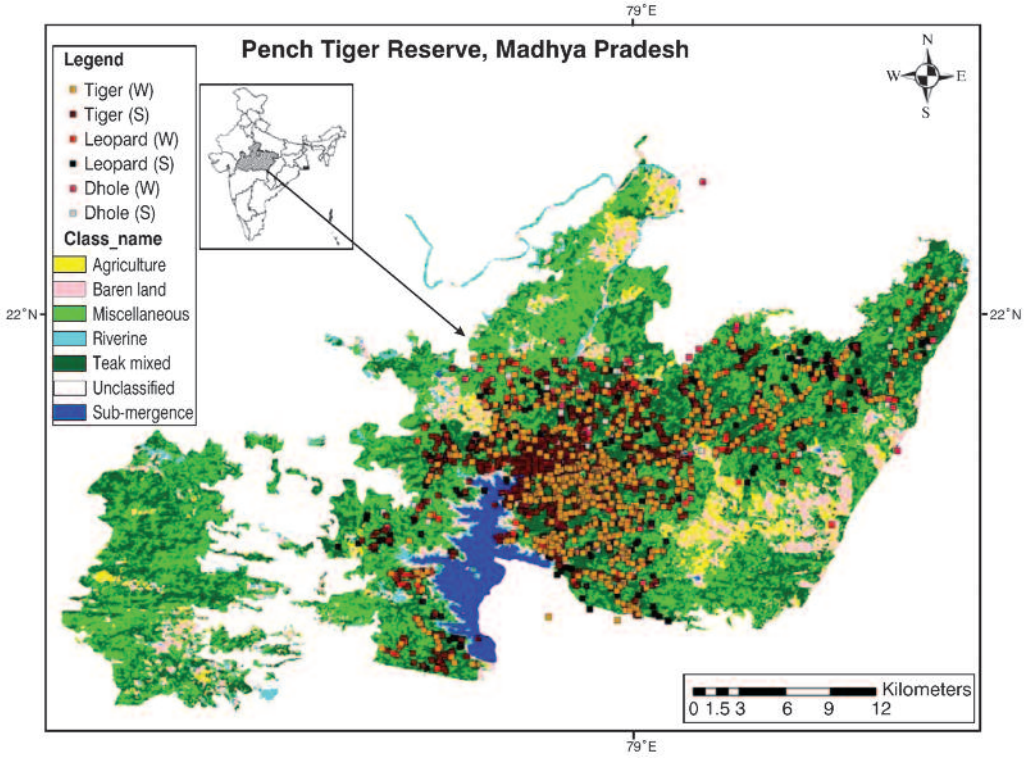

FIG. 1. Distribution of tiger, leopard and dhole signs on the land use and land cover map of Pench Tiger Reserve, Madhya Pradesh, India in winter (W) and summer (S).

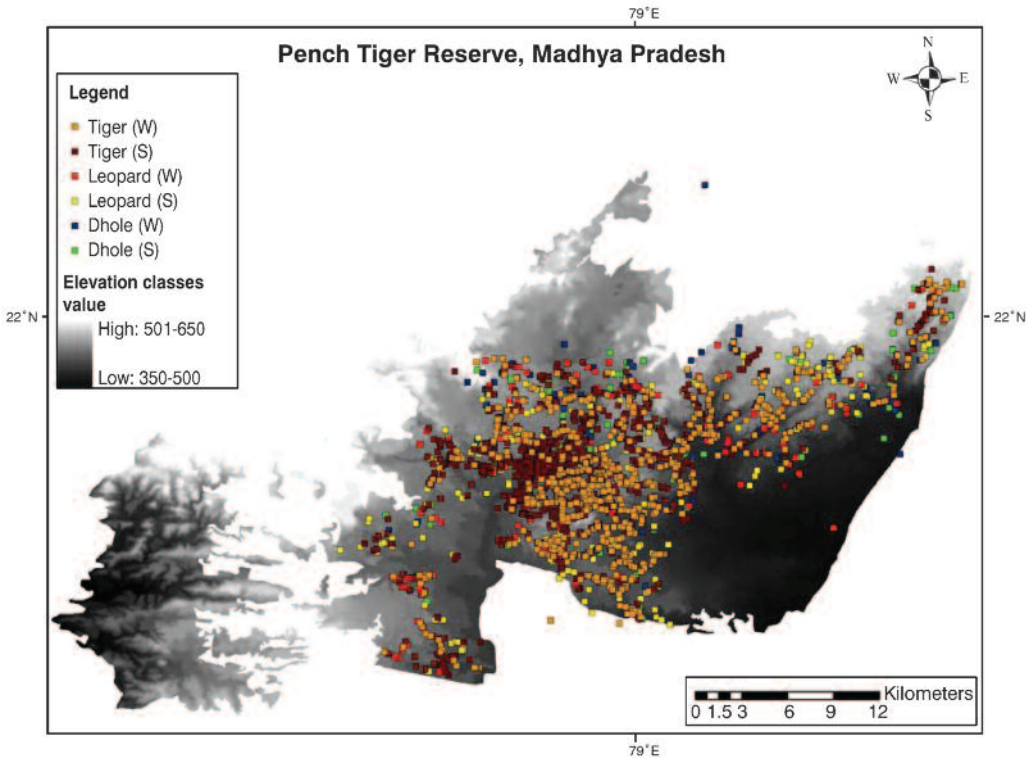

FIG. 2. Distribution of tiger, leopard and dhole signs on the different elevation classes of Pench Tiger Reserve, Madhya Pradesh, India in winter (W) and summer (S).

random points were found to be adequate to study habitat availabilities, as the curve was asymptotic at this point.

Habitat selection by tiger, leopard and dhole

Point locations (%) of each utilized habitat resources by these species in both winter and summer were compared with the available point locations (%) to study the habitat selection pattern (Neu *et al.*, 1974; Manly *et al.*, 2004). Confidence interval technique which involves the use of Bonferroni's Z statistic (Neu *et al.*, 1974) was carried out to verify which habitat types were preferred. If the proportion available for a given habitat class lies above or below the upper or lower boundary of the confidence interval then that vegetation is considered selected or avoided, respectively. The indices "- -", "++" and "**" provided the basis for ranking the relative habitat preference by all three carnivores among different habitat categories (Table 1 & 2). The G-test (Zar, 1984) was used to study seasonal habitat separation among three large carnivores in the study area.

RESULTS

A total of 1303 and 2238 locations of tiger evidence, 362 and 608 locations of leopard evidence and 264 and 324 locations of dhole evidence were recorded in winter and summer, respectively (Figs 1 & 2). The total effort for the present study was 1162 km in winter and 1674 km in summer. Significant difference (t-test, $p = 0.02$) was found between summer and winter use of habitats by large carnivores. We pooled data of same seasons across years as there was no significant difference (t-test, $p = 0.09$).

Land use and land cover

In winter, tiger utilized teak-mixed forest more than it's availability (++), utilized riverine and miscellaneous habitats in proportion to their availabilities (*); submergence, agriculture and barren lands were utilized less than their availabilities (-) (Table 1). In summer, tigers utilized riverine and submergence habitats more than their availabilities, utilized barren land and teak-mixed habitats in proportion to their availabilities and both agriculture and miscellaneous

TABLE 1. Utilization of different land use and land cover types by tiger, leopard and dhole in winter (W) and summer (S) in Pench Tiger Reserve, Madhya Pradesh between June 2006 and April 2011

Species	Land use and land cover classes	No. of random points in each habitat	Proportion available	No. of carnivore signs in each habitat (W)	Proportion used (W)	Lower limit (W)	Upper limit (W)	Intensity of use	No. of carnivore signs in each habitat (S)	Proportion used (S)	Lower limit (S)	Upper limit (S)	Intensity of use
Tiger	Sub-mergence	36	0.031	5	0.004	–0.001	0.008	-	114	0.051	0.039	0.063	++
	Riverine	24	0.021	39	0.029	0.017	0.042	*	189	0.084	0.069	0.100	++
	Miscellaneous	429	0.375	455	0.349	0.314	0.384	*	721	0.322	0.296	0.348	-
	Agriculture	39	0.034	1	0.001	–0.001	0.003	-	3	0.001	–0.001	0.003	-
	Barren land	149	0.130	59	0.045	0.030	0.060	-	256	0.114	0.097	0.132	*
	Teak mixed	467	0.408	744	0.571	0.535	0.607	++	955	0.426	0.399	0.454	*
Leopard	Sub-mergence	36	0.031	0	0	0.000	0.000	-	3	0.005	–0.003	0.012	-
	Riverine	24	0.021	1	0.003	–0.001	0.007	-	6	0.009	–0.001	0.020	-
	Miscellaneous	429	0.375	167	0.461	0.422	0.500	++	252	0.414	0.362	0.467	*
	Agriculture	39	0.034	0	0	0.000	0.000	-	4	0.006	–0.002	0.015	-
	Barren land	149	0.131	9	0.024	0.013	0.037	-	25	0.041	0.020	0.062	-
	Teak mixed	467	0.408	185	0.511	0.472	0.550	++	318	0.523	0.470	0.576	++
Dhole	Sub-mergence	36	0.031	0	0	0.000	0.000	-	1	0.003	–0.005	0.011	-
	Riverine	24	0.021	4	0.015	–0.005	0.035	*	6	0.018	–0.001	0.038	*
	Miscellaneous	429	0.375	110	0.416	0.337	0.497	*	129	0.398	0.326	0.470	*
	Agriculture	39	0.034	0	0	0.000	0.000	-	2	0.006	–0.005	0.018	-
	Barren land	149	0.131	9	0.034	0.005	0.064	++	11	0.033	0.007	0.060	-
	Teak mixed	467	0.408	141	0.534	0.453	0.615	++	175	0.541	0.467	0.613	++

TABLE 2. Utilization of different terrain types (elevation classes) by tiger, leopard and dhole in winter (W) and summer (S) in Pench Tiger Reserve, Madhya Pradesh, between June 2006 and April 2011

Species	DEM ranges (m)	Number of Random points in each categories	Proportion of available categories	No. of carnivore signs in each categories (W)	Proportion of used (W)	Lower limit (W)	Upper limit (W)	Intensity of use (W)	No. of carnivore signs in each categories (S)	Proportion of used (S)	Lower limit (S)	Upper limit (S)	Intensity of use (S)
Tiger	350-500	703	0.455	480	0.379	0.353	0.405	-	755	0.337	0.311	0.362	-
	501-600	843	0.545	786	0.621	0.595	0.647	++	1487	0.663	0.638	0.689	++
Leopard	350-500	703	0.455	182	0.501	0.472	0.530	++	296	0.486	0.457	0.515	++
	501-600	843	0.545	181	0.499	0.470	0.528	-	313	0.514	0.485	0.543	-
Dhole	350-500	703	0.455	117	0.437	0.377	0.496	**	144	0.442	0.382	0.502	**
	501-600	843	0.545	151	0.563	0.504	0.623	**	182	0.558	0.498	0.618	**

TABLE 3. G-test statistics for seasonal spatial separation between tiger, leopard and dhole in Pench Tiger Reserve, Madhya Pradesh

G-test statistics	Land use and Land cover (Winter)	Land use and Land cover (Summer)	Terrain or elevation (Winter)	Terrain or elevation (Summer)
G-adjusted	29.04	21.7	17.735	1.8959
G-critical	12.6	18.3	9.487	9.487
p-value	0.0001	0.01	0.001	0.754
d.f.	6	10	4	4

habitats were utilized less than their availabilities (Table 1). Leopard utilized both teak-mixed and miscellaneous forest types more their availabilities and utilized rocky-barren land and riverine forest more than their availability, whereas utilized both submergence and agricultural land less than their availabilities in winter. In summer, leopard utilized teak-mixed forest more than it's availability and utilized miscellaneous forest in proportion to its availability, whereas riverine, agriculture land, barren land and submergence habitat types were less utilized (Table 1). Dholes utilized both barren land and teak-mixed forests more than their availabilities and utilized riverine and miscellaneous forest in proportion to their availabilities, whereas no dhole evidence was obtained from submergence and agricultural land in winter. In summer, dholes utilized teak-mixed forests more than it's availability and utilized riverine and miscellaneous forests in proportion to their availabilities, whereas barren land, agricultural land and submergence areas were utilized less than their availabilities (Table 1).

Terrain

In both winter and summer tiger utilized elevation between 501 m and 650 m more than its availability, leopards utilized elevation between 350 m and 500 m more than its availability and dhole used both of these terrain types in proportion to their availabilities (Table 2).

Seasonal habitat separation among sympatric carnivores

A significant difference (G-test) was observed by all three carnivores while utilizing different land use and land cover types in both winter ($p = 0.0001$) and summer ($p = 0.01$), terrain types in winter ($p = 0.001$) whereas no significant difference was observed while utilizing different terrain types in summer ($p = 0.75$) (Table 3).

DISCUSSION

The accuracy of habitat use estimates depends on how well the underlying assumptions were met. Large carnivore selectively utilized the habitat, and the pattern of selection differed among seasons. These seasonal differences suggested that habitat selection changed over time. The present study supported the findings of earlier studies in Indian sub-continent that large carnivore prefer dense forested habitats for their different biological activities (Seidensticker, 1976; Biswas & Sankar, 2002; Edgaonkar, 2008; Jhala *et al.*, 2008). Both tigers and leopards are stealthy predator and stalk their prey from a certain distance before attacking (Hornocker, 1970; Seidensticker, 1976; Logan & Irwin, 1985). During present study, evidences of all three species were mostly observed in teak-mixed and miscellaneous forests (together > 90%) in both summer and winter. The utilization of both teak mixed and miscellaneous forest more than their availabilities by all three carnivores might be due to high abundance of sambar in these habitats. Acharya (1997) reported relatively higher heterogeneity both in tree composition and dense under storey found to be preferred habitat of sambar in the study area. The distribution of tiger evidences in hilly terrain (elevation 501-650 m) might be influenced by the distribution of gaur in this habitat (Acharya, 1997). Although there is high diet overlap between tiger, leopard and dhole reported in the study area, some diet segregation amongst them is also observed (Majumder *et al*., 2012). Tiger can hunt on larger body sized prey species such as gaur which is largely avoided by comparatively smaller body sized dhole and leopard (Ramesh, 2010; Majumder *et al*., 2012). In PTR, especially during summer, tiger used riverine (8.4%) and submergence (5.1%) areas more as compared to leopard (0.5% only in summer) and dhole (0.3% only in summer) (Table 1). This may be attributed to abundance of chital in both of these habitats (density 167 individuals per

km² from line transect). The fairly open canopy and availabilities of palatable grass species *Cynodon dactylon* probably attracted chital in both submergence (11.7 km²) and riverine habitats (12.5 km²). Though chital is also one of the major prey species for both leopards and dholes in the study area, majorly open riverine and submergence areas were less preferred by both of them to avoid inter-specific competition with comparatively larger body sized competitor; tiger. Thus, the habitat requirements of the prey combined with the prey preferences of each species also influenced space use of competing carnivores. Seidensticker (1976) found that, differences in use of habitat patches by tiger and leopard in Nepal was an important component of their ecological separation. Subtle differences in habitat use, possibly associated with avoidance, have also been documented between jaguar and puma in Peru (Emmons, 1987) and in Mexico (Aranda & Sánchez-Cordero, 1996). Avoidance can also magnify the effect of differential patch use (Ives & Dobson, 1987; Chesson & Rosenzweig, 1991). Our finding is also in accordance with the findings of several studies in African savannah where comparatively smaller body sized predators such as African wild dogs (*Lycaon pictus*) and hyenas (*Crocuta crocuta*) avoided the areas used by lions (*Panthera leo*) (Kruuk, 1972; Trikel & Kastberger, 2005; Webster *et al*., 2012; Darnell, 2012). Durant (2000) also reported that Serengeti cheetahs (*Acinonyx jubatus*) employ avoidance behaviour to reduce the risks of agonistic encounters with lion and hyena. Moehrenschlager *et al.* (2007) found that kit foxes were able to successfully avoid coyotes within relatively small areas indicating that sometimes smaller competitors may be able to co-exist with larger competitors separating their habitats.

Another probable reason for tiger largely utilizing the submergence area may be due to the availability of dense bushes of *Lantana camara* along the Pench river bank which acts as cover for rearing cubs during their early growing stage (< 2 years). The evaluation of denning sites (n = 20) of four breeding female tigers (one radio-collared and three non collared) in the intensive study area showed that, they were found in high prey biomass area (pooled biomass of chital, sambar, nilgai, gaur, wild pig and common langur was 9694.2 kg km^{-2} with a total effort of 618.6 km using line transect method), with no anthropogenic disturbance and availability of water in all seasons (< 200 m).

All three sympatric large carnivore species were observed to avoid agricultural habitats present in the fringes of forest boundary (Table 1). As studied by Smith (1993) in Nepal, tiger probably used agricultural habitat during their dispersal from the natal area. The rocky or barren lands were preferred by dholes during winter and the reason for the same was attributed to denning and rearing pups as reported by Acharya *et al.* (2007).

Differences in habitat use, either temporally or spatially, have been recognized as behavioural characteristics that may promote co-existence (Partridge, 1978). Majumder *et al.* (2012) reported the variation in temporal activity patterns among these large carnivores in the study area may largely lie in utilization of prey resources in different times (hours) of a day (leopard being nocturnal, tiger crepuscular and dhole diurnal). Our study revealed that a significant seasonal spatial separation between these three sympatric carnivores may allow their co-existence in PTR, similar to the co-existence pattern of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos (Scognamillo *et al.*, 2003). Many studies have also found that sympatric carnivores are able to co-exist by selecting different habitats (Seidensticker, 1976; Schaller & Crawshaw, 1980; Norton & Lawson, 1985; Konecny, 1989; Johnson *et al.*, 1996; Fedriani *et al.*, 1999).

Conservation implication

The study area offers a mosaic of ecological and habitat conditions, which effectively contributed to the maintenance of a rich assemblage of ungulates and primates in high numbers (Majumder *et al*., 2012). This high prey base along with different habitat conditions in the study area is ideal for the sustenance and growth of these three large sympatric carnivores. Our study area Pench is connected with two other source-population sites of large carnivores, i.e. Kanha Tiger Reserve and Satpura Tiger Reserve, and forms one of the important units of meta-population structure of tiger, leopard and dhole in Central Indian Landscape (Qureshi *et al*., 2006; Jhala *et al*., 2010). The present study gave insight on multiple large predator co-existence patterns in this human dominated landscape. Though the intensive study area is relatively undisturbed and no poaching of wild ungulate was recorded during the present study, there is continuous biotic pressure exert from the 99 villages located around the notified buffer zone of PTR, Madhya Pradesh (Qureshi *et al*., 2006). Protection of the habitat in Pench and surrounding areas is crucial for the survival of large carnivores in this landscape.

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