Diversity, Occupancy, and Spatio-temporal Occurrences of Mammalian Predators in Bhutan's Jigme Dorji National Park

Phuntsho Thinley
University of New England (Australia)

Paul D. Curtis
Cornell University

James Lassoie
Cornell University

Tshering Dorji
Forest Resources Planning and Management Division

BJNRD (2015), 2(1): 19-27

Bhutan Journal of Natural Resources & Development

Article

www.bjnrd.org

Open Access

ISSN 2409–2797 (Print)
ISSN 2409–5273 (Online)

doi: http://dx.doi.org/10.17102/cnr.2015.03

Diversity, Occupancy, and Spatio-temporal Occurrences of Mammalian Predators in Bhutan's Jigme Dorji National Park

Phuntsho Thinley[1], Stephen J. Morreale[2], Paul D. Curtis[2], James P. Lassoie[2], Tshering Dorji[3], Leki[3], Sonam Phuntsho[3], and Namgay Dorji[3]

Abstract

Spatio-temporal occurrences and distribution of a full complement of wild predators may provide insights into their ecology and niche partitioning, and thus may be invaluable for conservation of many rare species. A first comprehensive camera trapping effort, including 7,462 trap-days during fall and winter of 2011–2012 in the temperate and subalpine forests of Bhutan's Jigme Dorji National Park (JDNP), yielded 407 photographs of 12 species of wild predators belonging to 6 families. In the photographs, predator diversity was dominated by six felids, the most predominant being tiger (*Panthera tigris* Linnaeus) and Asiatic golden cat (*Pardofelis temminckii* Vigors and Horsfield). The photographs were further analysed using the programme PRESENCE to estimate patch occupancy and detection probability for each predator species. Overall, the yellow-throated marten (*Martes flavigula* Boddaert) was found to have the highest relative abundance index of 1.26. There were also seasonal differences in occurrence. Dholes (*Cuon alpinus* Pallas) had the highest occupancy estimates among all predators in both fall (92% ± *SE* 0.56) and winter (98% ± *SE* 0.52). Tiger occupancy was much higher in winter (56% ± *SE* 0.14) than during fall (18% ± *SE* 0.07). Of all the predators, dholes seemed to have the broadest spatial distribution with 47 images, spread widely among 25 camera stations. Although the predators were found to be sympatric, they were separated in their temporal niches. Tigers were mostly active during night, dholes during day, and leopards (*Panthera pardus* Linnaeus) during both day and night. Most predators occurred in all four major habitat types, but mixed conifer forest contained the highest diversity of wild predators. Through this study, the baseline occupancy of wild predators during both fall and winter were established in the park to support future monitoring programmes. This study underscores JDNP as an important conservation area for wild predators, most notably cat species.

Key words: Predator diversity, spatio-temporal occurrences, occupancy, human settlements, camera trap, large predators, medium-sized predators, Bhutan

Introduction

Spatio-temporal occurrences of a full complement of wild mammalian predators in a specific geographic location may provide insights into niche partitioning among sympatric predators (Bridges and Noss, 2011). Part of the reason for a paucity of information in this regard is due to the highly cryptic habits of most wild predators (Pettorelli *et al.*, 2010). However, the recent proliferation in the use of camera traps to study terrestrial animals (Tobler *et al.*, 2008) has enabled wildlife researchers to enter the realm of cryptic animals (Nichols *et al.*, 2011), and to accelerate the discovery of habitat use and activity patterns, and provide essential information for their conservation. Accordingly, proper design of camera trap studies may provide valuable information on the occurrence of elusive animals in specific locations and habitats, at particular times of day and season. For wild predators, camera trap and occurrence data may indeed provide useful information concerning habitat use, degree of habitat overlap, and activity patterns (Sanderson, 2010). Such studies may also reveal information about the diversity and relative abundance of predators, aiding wildlife managers and

[1]RNR-RDC Yusipang, Department of Forests and Park Services, Thimphu, Bhutan; Corresponding Author: pt96@cornell.edu
[2]Department of Natural Resources, Cornell University, Ithaca, New York, 14853, USA
[3]Jigme Dorji National Park, Bhutan

Received Jun. 2015. Accepted Aug. 2015

conservationists in assessing the conservation status and management of high profile species.

Bhutan, a tiny Himalayan nation, is considered to be a biodiversity hotspot (MOAF, 2009); yet, it is virtually unexplored in terms of biodiversity studies. Because the country lies at the crossroad of two major biogeographic realms, the Palearctic and the Indo-Malayan (MOAF, 2005), about 36 species of mammalian predators are expected to be present in the country (Wangchuk *et al.*, 2004). However, the existence of some species is yet to be confirmed. In addition, most of Bhutan's protected areas have not been fully surveyed; so, a comprehensive list of species present in each is unavailable. With the recent availability of camera traps, conservationists have already identified the occurrence of some rare and cryptic species in several areas (Wang and Macdonald, 2009; Tempa *et al.*, 2013). But, other than these studies, explorations have been sporadic and incidental, and were not systematically designed to allow for exhaustive inventories of numerous species. This greatly limits understanding the diversity of wild animals in the unexplored regions of Bhutan and the seasonal distribution of important animals in diverse habitats and locations.

Therefore, the objectives of this study were to: 1) to understand the diversity of predators in the largely unexplored temperate and subalpine forests of Bhutan's Jigme Dorji National Park; 2) calculate baseline occupancy for large predators; and 3) examine predators' activity patterns and habitat selection.

Materials and Method

Study area

Covering approximately about 4,316 km^2, Jigme Dorji National Park (JDNP) is the second largest protected area in Bhutan (Figure 1). Elevations in the park range from 1,200 to 7,200 m above mean sea level. Due to its location in the upper Himalayan Ranges, much of the park has mountainous and rugged topography. Diverse topographic features, in addition to a wide altitudinal range and steep slopes, have yielded seven major vegetation types in the park. Much of the areas above 4,000 m are dominated by alpine habitats such as meadows, scrub, and rocky outcrops. Areas below 4,000 m are mostly dominated by sub-alpine forests, comprised of birch (*Betula utilis* Don), Rhododendron thickets, juniper (*Juniperus* sp.) woodlands, and fir (*Abies densa* Griffith) forests. These areas are also dominated by mixed-conifer forests, comprised of pine (*Pinus wallichiana* Jackson) and broadleaved forests, which are predominantly covered with cool and warm broadleaved trees. The park spans over 5 *dzongkhags* (administrative districts) and 15 *geogs* (administrative blocks) that encompass 35 villages. A majority of the park residents maintain subsistence lifestyles, either as agro-pastoralists in the lowlands or pure pastoralists in the uplands. Rich in culture and biodiversity, the park is aptly called a trekker's paradise, and about 3,000 international tourists visit the park annually. The park forms the critical watershed for four major rivers in the country: *Pa Chhu*, *Wang Chhu*, *Pho Chhu*, and *Mo Chhu* (Thinley *et al.*, 2015c).

Design of camera trap surveys

The study was originally designed to inventory tigers in the park (Thinley *et al.*, 2015b), and this design influenced the location of the camera traps. At the outset, the first author trained park rangers and their support staff in identification of tiger evidence, setting up camera traps, and the use of Global Positioning System (GPS) units. Based on an ecology-based niche model output of suitable areas for tigers (Thinley, 2008), the entire park was divided into suitable and unsuitable areas for tiger, with suitable areas encompassing approximately 1,620 km^2 (Figure 1). Using an area close to the smallest reported tiger home range size of 15 km^2 (Karanth *et al.*, 2011), a grid of 4 x 4 km cell size was overlaid on the map of suitable tiger areas.

Within the entire suitable tiger area, a reconnaissance survey was conducted by park rangers and their support staff across all grid cells. First, identifiable human and animal trails in the area were traversed to search for direct evidence of tiger presence, such as scat, tracks, scratch marks, rubbings, scent marks, carcasses, calls, and sightings. Additionally, reports of livestock killed by tigers, and local people's knowledge also were recorded to help identify areas with the highest probability of tiger occurrence. Based on this preliminary survey, 31 grid cells containing areas with the most evidence were identified for stationing camera traps (Figure 1). An additional 10 grid cells in the south-eastern region of the park were added to the study. Although this region was not part of the initial survey, tiger presence was expected there because of the prevailing highly suitable tiger habitat (Thinley, 2008).

An average spacing of 3 km was maintained between the camera traps, which is enough to capture all wide and narrow-ranging predators in the study area (Johnson *et al.*, 2009). Cameras were operational for 182 days covering two seasons: fall

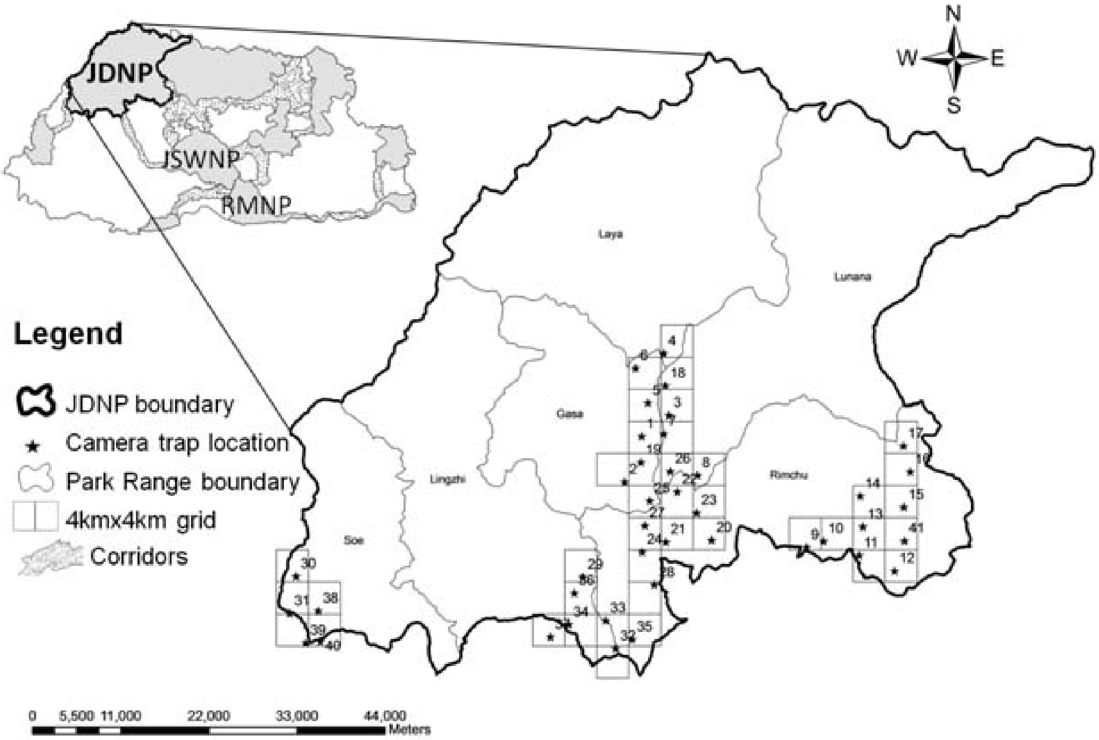

Figure 1. Location of the study area and camera traps stationed in areas below 4,200 m within JDNP during 1 September, 2011 to 29 February, 2012

(September – November, 2011) and winter (December, 2011 – February, 2012). The camera trapping efforts totalled 7,462 trap-days, with 3,731 trap-days in each season. The camera stations were visited by park staff during two-week intervals to change batteries and memory cards.

Data management and analysis

To organise camera trap images and ancillary data, the programme Camera Base 1.5, developed by Tobler (2012) in Microsoft Office Access, was used. The programme was set up to automatically estimate sun-rise and sun-set times once the Greenwich Mean Time (GMT) and the geographical coordinates of the study sites were entered. All images were organised by different seasons, locations, dates, and times. In Camera Base, a time gap of one hour for photographs was considered to be independent. In other words, all photographs of the same species captured within this time period by the same camera on the same day were considered to be a single capture event. The programme's analytical tool was also used to analyse the activity patterns of animals. To process a map of habitats in the park, GIS programme ArcMap 9.3 (Environmental Systems Research Institute, Inc., California, USA) was used to extract habitat types from the landuse map of Bhutan 2011. Locations of camera traps were overlaid on the habitat map to determine which individuals of a species were found in a particular habitat.

The animal capture data from Camera Base were exported to programme PRESENCE 5.8 (Hines, 2013) to estimate patch occupancy and detection probability for each predator species. The programme accounted for false absences, which could have been caused by poor animal detection, through repeated sampling (MacKenzie *et al*., 2006). A constant P (detection probability) model for each season of the year was selected, and each calendar-year season was considered as a survey season and every 15 trap-days was regarded as a sampling occasion in the model. The populations of all species were assumed to be closed in each season without any birth, deaths, immigration, and emigration. In fact, there were no reports of poaching and other sources of mortality during the entire study period, thus supporting this assumption. Occupancy for species whose total number of photographs was less than five were not calculated, because the programme would yield meaningless estimates.

Results and Discussion

Diversity, occupancy and relative abundances of predators

A total of 407 independent photographs of wild predators were recorded from 35 of 41 camera traps

(Table 1). This included 12 species of wild mammalian predators belonging to 6 families, all within the temperate and subalpine areas of JDNP. The remaining six cameras recorded images of other biota, including wild and domestic herbivores and people. Of the 12 predators, 6 belonged to the cat family (*Felidae*) and 2 to the dog family (*Canidae*). In addition, there was one predator representing the families *Ursidae*, *Prionodontidae*, *Viverridae*, and *Mustelidae*. Two species were listed as 'endangered', three were 'vulnerable', and two were 'threatened' on the IUCN (International Union for Conservation of Nature) Red List. The remaining five predators were classified as least concern (IUCN, 2015). Five species, namely clouded leopard (*Neofelis nebulosa* Griffith), tiger, leopard, leopard cat (*Prionailurus bengalensis* Kerr), and Himalayan black bear (*Ursus thibetanus* [Baron] Cuvier) were listed in Schedule I of Forest and Nature Conservation Act of Bhutan 1995, which accords them the highest protection status.

The yellow-throated marten was the most photographed species (*n* = 94 independent images), with the highest relative abundance index of 1.26 (Table 1), and it was the most abundant predator species in JDNP, followed by the Himalayan black bear (*n* = 78 independent images) with a relative abundance index of 1.05, and the Asiatic golden cat (*n* = 60 independent images) with a relative abundance index of 0.80. Among the large felids, tiger was the most abundant species (*n* = 47 independent images) with a relative abundance index of 0.63. The clouded leopard was the least abundant cat species (*n* = 4 independent images) with a relative abundance index of 0.05. Contrary to expectations, only 14 independent images of leopards were obtained, leading to a low relative abundance index of 0.l9. Dholes (*n* = 47 independent images) exhibited a relative abundance index of 0.63, equal to that of tigers. Spotted linsang (*Prionodon pardicolor* Hodgson) and masked palm civet (*Paguma larvata* Smith) were captured in very low frequency, with relative abundance indices of 0.01 and 0.04, and with one and three images, respectively.

Generally, occupancy estimates for wild predators were higher in fall than during winter, with the exception of tiger and dholes (Table 1). Dholes had the highest occupancy estimates among all predators for both fall (92% ± *SE* 0.56) and winter seasons (98% ± *SE* 0.52). Tiger occupancy was much higher in winter (56% ± *SE* 0.14) than during fall (18% ± *SE* 0.07). In contrast, golden cat occupancy was more than twice as high in fall (68% ± *SE* 0.08) than during winter (33% ± *SE* 0.11). The occupancy estimates for leopard cats in fall (16% ± *SE* 0.08) and winter (17% ± *SE* 0.08) were almost equal, whereas for leopards, the estimate was 0% in winter but 33% ± *SE* 0.29 in fall.

Lack of reliable data on the total number of animals, their relative abundance, activity patterns, and habitat types has been the major impediment to scientific management of animals and habit conservation (Balmford *et al*., 2005). Taking advantage of modern camera traps, this study has not only inventoried and confirmed the presence of 12 species of mammalian predators in JDNP, but also established the baseline data for their habitat use, occupancy, detection probability, and activity patterns. Such information provides a scientific basis for managing and monitoring changes in such important state variables for predators through time and various seasons.

A separate camera trap study has been completed in areas above 4200 m to document the occurrence of wild predators. Snow leopard (*Panthera uncia* Schreber) and manul or Pallas's cat (*Otocolobus manul* Pallas) were documented at those high elevations (Thinley, 2013; Thinley *et al*., 2015a). This brings the total number of wild predators in JDNP to 14.

However, readers are cautioned while interpreting occupancy estimates from Table 1 for predators other than tiger, leopard, and dhole, because the camera trap study was designed for wide-ranging animals, and hence most of the individuals belonging to smaller-ranging species may not have been captured on camera traps. Moreover, the camera trap shyness or avoidance behaviors of smaller predators could not be determined in this study. Such a behavioral trait might affect detection probability of the animals, and may in turn affect the occupancy estimates.

Underscoring its important role as an umbrella species for habitat conservation, tigers in JDNP coexisted with five species of other wild felids, bears, dholes, and small predators in the park below 4,200 m. However, comparatively low occupancy estimates for other felids species were noted, including the leopard. Such a pattern was attributed to a relatively high abundance of large, dominant predators, such as tigers. This finding corroborates with those in the south Asian region that wherever tigers are abundant, leopards are few (Seidensticker, 1976; Odden *et al*., 2010).

Tigers and leopards were not detected in any of the 10 camera traps stationed in the southeastern part of the park where they were expected to occur based on the presence of their principal prey species, and suitable habitat. This is a red flag for the park management and wildlife conservation agencies.

Table 1. Wild predator species photographed at 35 camera traps stationed in Bhutan's JDNP from 1 September 2011 to 29 February, 2012

Species by Family, common name, and scientific name	No. of IDPT[a] images	RAI[b]	Captures in trap sites (%)	IUCN status 2012 [c]	Fall (Sep. - Nov. 2011) Naïve occup[d]	Fall Occup. (SE)[e]	Fall P (SE) [f]	Winter (Dec. 2011- Feb. 2012) Naïve occup[d]	Winter Occup. (SE)	Winter P (SE)
Felidae										
Tiger *Panthera tigris*	47	0.63	18 (44)	EN	0.15	0.18 (0.07)	0.25 (0.09)	0.39	0.56 (0.14)	0.18 (0.05)
Leopard *Panthera pardus*	14	0.19	8 (20)	NT	0.12	0.33 (0.29)	0.07 (0.07)	0.10	0	0.02 (0.01)
Clouded leopard *Neofelis nebulosa*	4	0.05	4 (10)	V	0.03	0	0	0.07	0	0.01 (0.01)
Asiatic golden cat *Pardofelis temminckii*	60	0.80	17 (41)	NT	0.29	0.68 (0.32)	0.09 (0.05)	0.24	0.33 (0.11)	0.19 (0.06)
Marbled cat *Pardofelis marmorata*	21	0.28	6 (14)	VU	0.05	0	0.01 (0.01)	0.1	0.10(0.05)	0.44 (0.11)
Leopard cat *Prionailurus bengalensis*	35	0.47	8 (20)	LC	0.12	0.16 (0.08)	0.19 (0.09)	0.12	0.17 (0.08)	0.19 (0.09)
Canidae										
Dhole *Cuon alpinus*	47	0.63	25 (61)	EN	0.29	0.92 (0.56)	0.06 (0.04)	0.42	0.98 (0.52)	0.09 (0.02)
Red fox *Vulpes vulpes*	3	0.04	2 (5)	LC	0	0	0	0.05	0	0.01 (0.01)
Ursidae										
Himalayan black bear *Ursus thibetanus*	78	1.05	19 (46)	VU	0.32	0.43 (0.12)	0.19 (0.06)	0.27	0.34 (0.10)	0.23 (0.06)
Mustelidae										
Yellow-throated marten *Martes flavigula*	94	1.26	19 (46)	LC	0.32	0.43 (0.12)	0.20 (0.06)	0.32	0.37 (0.09)	0.27 (0.06)
Prionodontiade										
Spotted linsang *Prionodon pardicolor*	1	0.01	1 (2)	LC	0	0	0	0.02	0	0
Viverridae										
Masked palm civet *Paguma larvata*	3	0.04	3 (7)	LC	0.02	0	0	0.05	0	0.01 (0.01)
TOTAL	407									

[a] All photographs of the same species captured within one hour by the same camera on the same day were considered to be independent (IDPT)

[b] Relative abundance index (RAI) was calculated as the number of independent images taken per 100 trap days

[c] E = Endangered; NT = Not Threatened; VU = Vulnerable; LC = Least Concern (IUCN, 2015)

[d] Naïve occupancy is the proportion of camera trap stations where the species was detected at least once and it doesn't account for the detection probability (P)

[e] Estimated occupancy of the species which factors in detection probability (P)

[f] Detection probability in the study area for each season

During the course of this study, several photographs of people with bows and arrows were obtained at two camera stations, suggesting the potential for poaching and human disturbance in that region of the park.

Occurrences by habitat, elevation, and space

All four major habitat types prevalent in the study area were occupied by tigers, leopard cats, dholes, yellow-throated martens, and black bears, whereas clouded leopards, leopards, marbled cats, golden cats, and palm civets were observed in only broadleaf and mixed-conifer forests (Figure 2). The leopard cat was not found in fir forest, and the red fox (*Vulpes vulpes* Linnaeus) was found in both fir and mixed-conifer forests. The only spotted linsang was observed in mixed-conifer forest. Tigers and black bears occurred mostly in mixed-conifer forest and least in blue pine forest. Likewise, dholes occurred mostly in mixed-conifer forest and least in fir forest. Yellow-throated martens and Asiatic golden cats were observed in mostly broadleaf and mixed-conifer forest. Among the 4 forest types, only mixed-conifer forest contained all of the species of wild predators observed, with a total of 230 independent images. The broadleaf forest had moderate diversity, containing148 independent images of 10 predator species. Fir forest had the least diversity of predators, with only 14 images of 4 species.

Tigers, dholes, bears, leopard cats, and martens were photographed by the camera trap 31 stationed at an elevation of 4,105 m, the highest elevation in the study area. Bears were found at all elevations, ranging from 2,063 to 4,105 m. The highest elevation for leopards, golden cats, clouded leopards, and marbled cats appeared to be 3,488 to 3,810 m, where as the lowest elevation for red fox was 3,681 m.

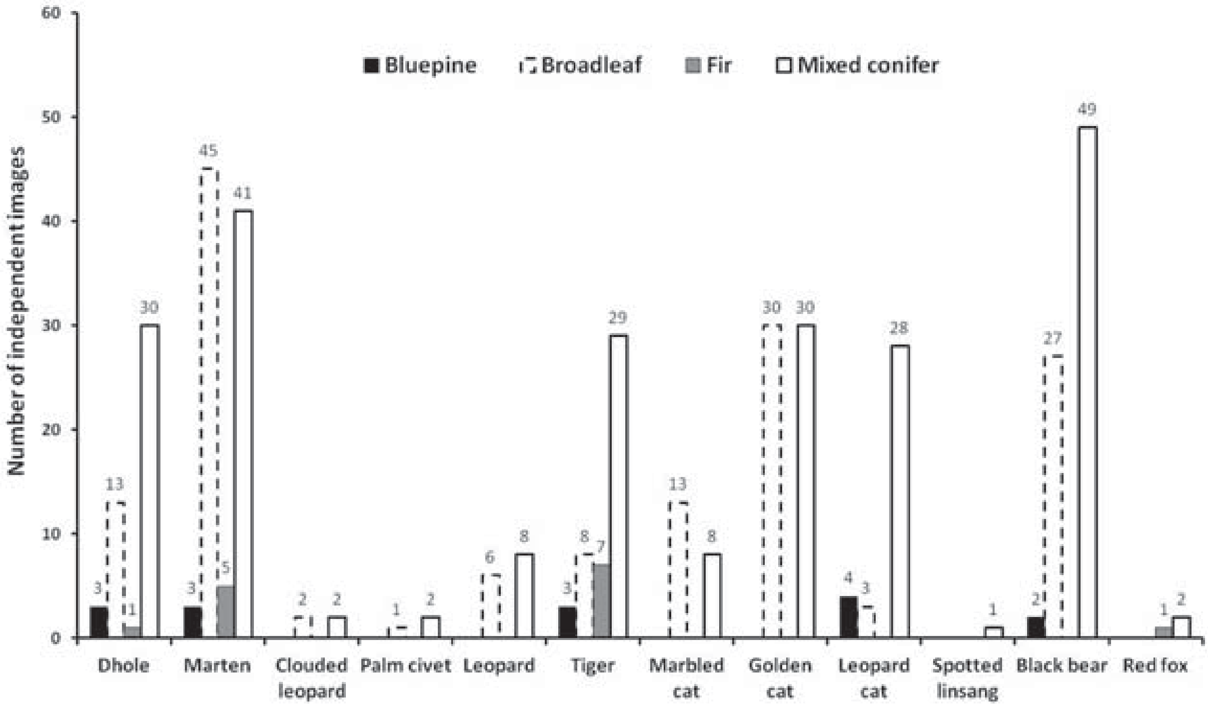

Figure 2. Patterns of habitat use by 12 species of wild predators in JDNP during 1 September, 2011 to 29 February, 2012

Spatially, dholes seemed to have the largest spatial coverage of all the predators, with 47 independent images spread widely across 25 camera stations (Table 1). Next were the yellow-throated marten and the Himalayan black bears, each captured at 19 stations. Among the wild cats, tigers and golden cats appeared to have the widest spatial coverage, with images captured on 18 and 17 camera traps, respectively. Leopards and leopard cats were captured on eight cameras each, marbled cats (*Pardofelis marmorata* Martin) on six cameras, and clouded leopard on four cameras.

There was much spatial overlap of species, including tigers and leopards, which were captured on the same camera trap at four separate trap stations (number 3, 22, 34, and 36). Tigers were also found sharing the same space with dholes and golden cats at 15 camera traps. Likewise, leopards were also found sharing space with these two medium-sized carnivores at seven camera traps. Among the medium-sized carnivores, dholes and golden cats were captured on the same camera trap at 12 trap stations, indicating a high degree of range overlap. The range of dholes also appeared to overlap with that of marbled cats, as indicated by photographs of both carnivores at five separate trap stations. None of the camera traps photographed all 12 species of predators at the same camera trap station. Cameras 1 and 3 photographed the most predator species (n = 7), while Camera 21 photographed only bears, and camera 20 photographed only dholes.

In contrast to findings in this study, Wang and Macdonald (2009) suggested no overlap of space use by tigers and leopards in Jigme Singye Wangchuck National Park (JSWNP) located in central Bhutan (Figure 1). However, range overlap between tigers and leopards in Bhutan was also observed by Tempa *et al*., (2011) in Royal Manas National Park (RMNP). Seidensticker (1976) also reported habitat overlap between tigers and leopards in Nepal's Royal Chitwan National Park, where they were separated by at least 125 m. Further, Karanth and Sunquist (2000) found that tigers, leopards, and dholes coexisted in the tropical forests of Nagarhole, India, and they could not find any evidence of spatial exclusion among these predators.

Occurrences by time of day and season

Tigers seemed to be mostly active from 1700 hours through 0500 hours (Figure 3). They were occasionally photographed during late morning, at around 0800 hours (n = 3 images) and late afternoon at around 1400 hours (n = 2 images). In contrast, dholes were active mostly during the day from noon to 1700 hours, and somewhat active during morning from 0600 to 1100 hours. No photographs of dholes were captured from 1900 till 0500 hours. Unlike tigers and dholes which exhibited specific activity periods, leopards and golden cats appeared to be active throughout much of the day and night, although leopards appeared to be absent, and presumably resting between 2200 and 0300 hours. Among the

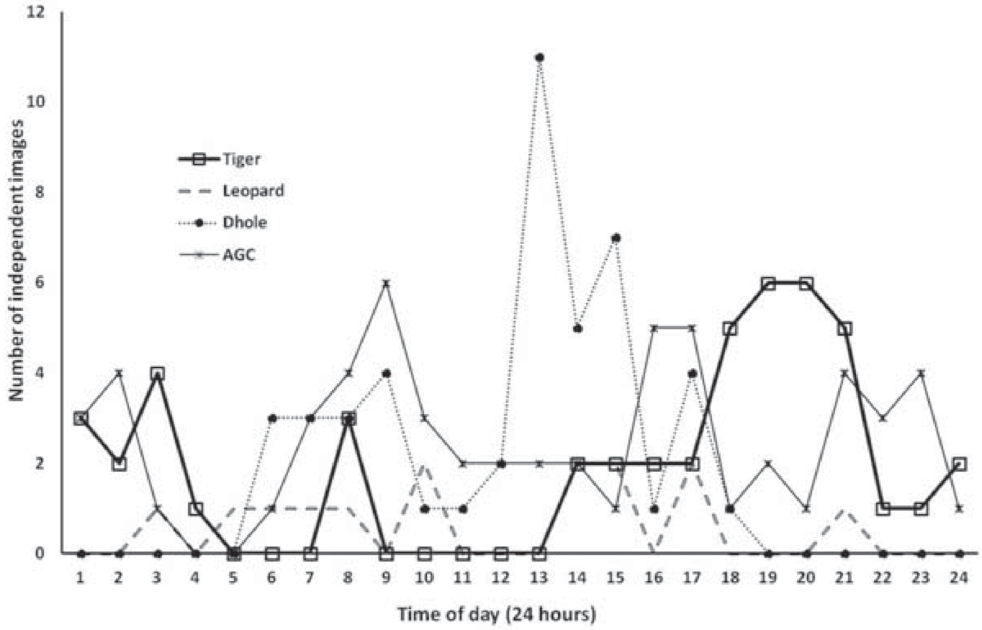

Figure 3. Activity patterns of four wild predators based on the number of independent photographs recorded on cameras during 24 hours in Bhutan's JDNP during 1 September, 2011 to 29 February, 2012

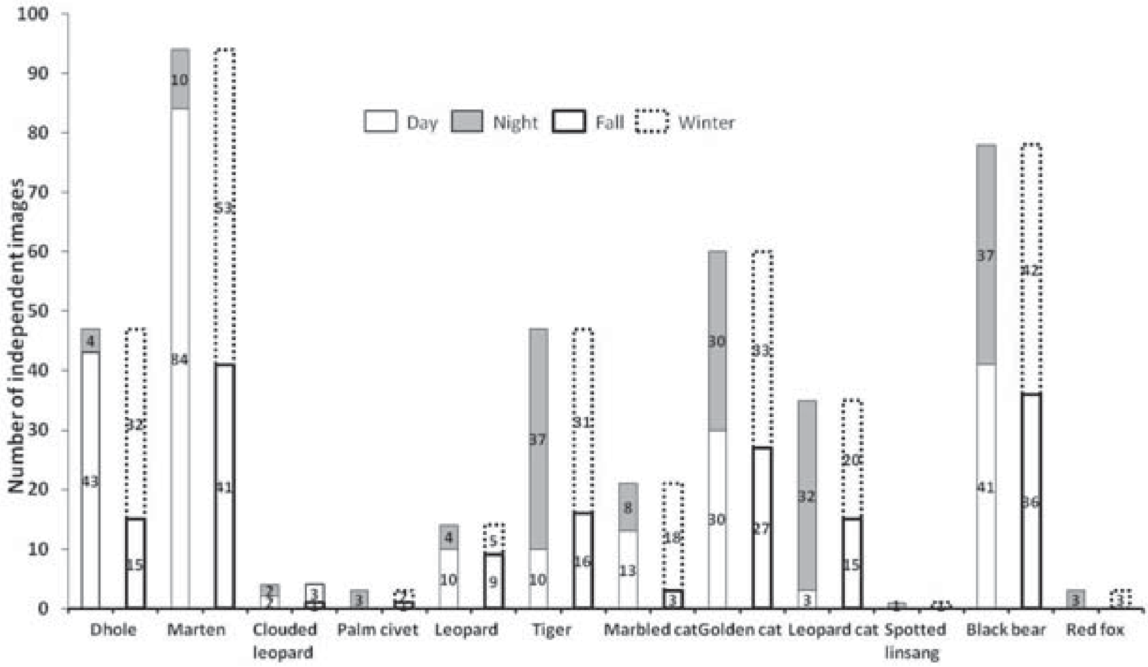

Figure 4. Temporal separation of wild predators by day and season in Bhutan's JDNP during 1 September, 2011 to 29 February, 2012

small felids, leopard cats appeared to be active during late evening until early morning (1800 to 0400 hours), although some images of them were taken from 0700 to 1100 hours. Marbled cats and bears were active during both day and night. Yellow-throated martens were mostly active between 0400 and 2300 hours. Activity patterns could not be established for the rest of the predators due to insufficient number of independent images.

There were seasonal patterns of occurrence too, based on the number of independent images obtained in each season. Tigers, leopard cats, and marbled cats were more active during winter than fall (Figure 4). Leopards were most active during fall. Golden cats were equally active during both the seasons. Dholes were more active during winter than fall, while bears and martens seemed to be equally active during both seasons. Red foxes were recorded three times, only in winter, and a spotted linsang was seen only, and that was in winter.

Conclusion

Through this camera trap study, the existence of several rare and endangered wild cat species in JDNP was discovered. Their existence in various habitat types and seasons, along varying elevation gradients, and during different time periods on a 24 hour scale were also documented. Such findings would contribute to solving human-predator conflicts through greater understanding of predators' habitat selection, and activity patterns in the park. For instance, knowledge of predator activity pattern in different habitat types would help farmers guard their cattle against different predators in different times of a day.

This study, along with a separate camera trap study in areas above 4,200 m of the park documenting the occurrence of the endangered snow leopard and manul highlights JDNP as one of the prime conservation areas for wild predators, particularly wild felids, in the upper Himalayan region of Bhutan and Eastern Himalayas region. Therefore, conservation efforts should be focused on protecting predators through mitigation of human-predator conflicts and through habitat protection.

Acknowledgement

The authors immensely thank the Government of Bhutan, particularly the Ministry of Agriculture and Forests, for kindly permitting to conduct this study as part of the management zoning exercise for JDNP. World Wildlife Fund, Bhutan Programme is duly acknowledged for generously supporting field activities and monitoring programmes. We sincerely thank and deeply appreciate the sacrifices and dedications demonstrated by park staff of Soe, Lingzhi, Rimchhu, Lunana, Laya, and Gasa Park Ranges in JDNP while conducting the camera trap survey. Without their help, a research project of this magnitude would not have been possible. We also immensely thank Prof. Stephen D. DeGloria of the Department of Crop Soil and Science, Cornell University, and Prof. D. B. Gurung of the College of Natural Resources of the Royal University of Bhutan for their comments and edits.

References

Balmford, A., Crane, P., Dobson, A.P., Green, R.E., and Mace, G.M. (2005). The 2010 challenge: data availability, information needs and extraterrestrial linsights. *Philosophical Transactions of the Royal Society of London, Series B*, 360: 221-228. doi:10.1098/rstb.2004.1599

Bridges, A.S., and Noss, A.J. (2011). Behavior and Activity Patterns. In *Camera Traps in Animal Ecology: Methods and Analyses*, eds. A.F. O'Connell, J.D. Nichols, and K.U. Karanth, pp. 57-69. Springer, New York, United States.

Hines, J.E. (2013). PRESENCE – Software to estimate patch occupancy and related parameters. USGS-PWRC. <http://www.mbr-pwrc.usgs.gov/software/presence.html>. Accessed 1 July 2013.

IUCN. (2015). *The IUCN Red List of Threatened Species. Version 2015.1*. <http://www.iucnredlist.org>. Accessed 1 June 2015.

Johnson, A., Vongkhamheng, C., and Saithongdam, T. (2009). The diversity, status and conservation of small carnivores in a montane tropical forest in northern Laos. *Oryx*, 43: 626-633. doi:10.1017/S0030605309990238

Karanth, K.U., Nichols, J.D., and Kumar, N.S. (2011). Estimating tiger abundance from camera trap data: Field surveys and analytical issues. In *Camera Traps in Animal Ecology: Methods and Analyses*, eds. A.F. O'Connell, J.D. Nichols, and K.U. Karanth, pp. 97-117. Springer, New York, United States.

Karanth, K.U., and Sunquist, M.E. (2000). Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. *Journal of Zoology*, 250: 255-265.

MacKenzie, D.L., Nichols, J.D., Royle, J.A., Pollok, K.H., Bailey, L.L., and Hines, J.E. (2006). *Occupancy estimation and modeling: Inferring patterns and dynamics of species cccurrence*. Academic Press, London, United Kingdom.

MoAF. (2005). *Tiger action plan for the Kingdom of Bhutan 2006-2015*. Kuensel Corporation Ltd., Thimphu, Bhutan.

MoAF. (2009). *Biodiversity action plan 2009*. Kuensel Corporation Ltd., Thimphu, Bhutan.

Nichols, J.D., Karanth, K.U., and O'Connell, A.F. (2011). Science, conservation, and camera traps. In *Camera Traps in Animal Ecology: Methods and Analyses*, eds. A.F. O'Connell, J.D. Nichols, and K.U. Karanth, pp. 45-56. Springer, New York, United States.

Odden, M., Wegge, P., and Fredriksen, T. (2010). Do tigers displace leopards? If so, why? *Ecological Research*, 25: 875-881. doi: 10.1007/s11284-010-0723-1

Pettorelli, N., Lobora, A.L., Msuha1, M.J., Foley, C., and Durant, S.M. (2010). Carnivore biodiversity in Tanzania: revealing the distribution patterns of secretive mammals using camera traps. *Animal Conservation*, 13: 131-139. doi: 10.1111/j.1469-1795.2009.00309.x

Sanderson, J. (2010). The art and zen of camera trapping. In *Conservation in the 21st century: Gorillas as a case study*, eds. T.S. Stoinski, H.D. Steklis, and P.T. Mehlman, pp. 160-169. Springer, New York, United States.

Seidensticker, J. (1976). On the ecological separation between tigers and leopards. *Biotropica*, 8: 225-234.

Tempa, T., Heebblewhite, M., Mills, L.S., Wangchuk, T.R., Norbu, N., Wangchuk, T., Nidup, T., Dendup, P., Wangchuk, D., Wangdi, Y., and Dorji, T. (2013). Royal Manas National Park, Bhutan: a hot spot for wild felids. *Oryx*, 74: 207-210.

Tempa, T., Norbu, N., Dhendup, P., and Nidup, T. (2011). *Results from a camera trapping exercise for estimating tiger populations size in the lower foothills of Royal Manas National Park*. Kuensel Corporation, Thimphu, Bhutan.

Thinley, P. (2008). *Design and application of a new conservation paradigm to tiger conservation in Bhutan*. MSc thesis, Cornell University, Ithaca, New York, United States.

Thinley, P. (2013). First photographic evidence of a Pallas's cat in Jigme Dorji National Park, Bhutan. *CatNews*, 58: 27-28.

Thinley, P., Dagay, Leki, Dorji, P., Namgyel, C., Yoenten, S., Phuntsho, and Dorji, T. (2015a). *Estimating snow leopard (Panthera uncia) abundance and distribution in Jigme Dorji National Park using camera traps: A technical report*. Kuensel Corporation Ltd., Thimphu, Bhutan.

Thinley, P., Dorji, T., Leki, Phuntsho, S., Dorji, P., Phuntsho, and Namgay, D. (2015b). *Estimating wild tiger (Panthera tigris) abundance and density using a spatially-explicit capture-recapture model in Bhutan's Jigme Dorji National Park*. Department of Forests and Park Services, Thimphu, Bhutan.

Thinley, P., Tharchen, L., and Dorji, R. (2015c). C*onservation management plan of Jigme Dorji National Park for the period January 2015 - December 2019: biodiversity conservation in pursuit of Gross National Happiness*. Department of Forests and Park Services, Thimphu, Bhutan.

Tobler, M.W. (2012). Camera Base, Version 1.6. <http://www.atrium-biodiversity.org/tools/camerabase>. Accessed 1 December 2013.

Tobler, M.W., Carrillo-Percastegui, S.E., Leite Pitman, R., Mares, R., and Powell, G. (2008). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*, 11: 169-178. doi: 10.1111/j.1469-1795.2008.00169.x

Wang, S.W., and Macdonald, D.W. (2009). The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biological Conservation*, 142: 606-613. doi: 10.1016/j.biocon.2008.11.023

Wangchuk, T., Thinley, P., Tshering, K., Tshering, C., Yonten, D., Pema, B., and Wangchuck, S. (2004). *A field guide to the mammals of Bhutan*. Royal Government of Bhutan, Thimphu, Bhutan.