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Activity patterns and spatial co-occurrence of sympatric mammals in the moist temperate forest of the Kashmir Himalaya, India

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Abstract. Little is known about the activity pattern and co-occurrence of mammalian species coexisting sympatrically in the rugged terrains of the Himalaya. By using camera traps we quantified diel activity patterns and temporal overlap as well as probabilistic model of spatial species co-occurrence amongst eight species. The jungle cat and the Indian porcupine tended to be strictly nocturnal whereas the leopard cat and the red fox were primarily nocturnal and crepuscular, yellow-throated marten was diurnal. The Asiatic black bear, leopard and the hangul showed no clear pattern. We found highest temporal overlap (Δ_1 = 0.84, 95%CI = 0.54-0.86) between leopard and Asiatic black bear followed by pairs between red fox and leopard cat (Δ_1 = 0.83, 95%CI = 0.72-0.91) and jungle cat (Δ_1 = 0.82, 95%CI = 0.60-0.91). The lowest temporal overlap was found between yellow-throated marten and Indian porcupine (Δ_1 = 0.11, 95%CI = 0.08-0.20). The results from probabilistic pairwise species co-occurrence analysis suggest that out of 28 possible species pairs 25 had random associations and one pair was unclassifiable. The remaining two species pairs had positive associations of co-occurrences between leopard cat and hangul ($P_{gt} < 0.05$) and Indian porcupine and hangul ($P_{gt} < 0.05$). Our results provided new insights into this unique community of mammals of the western Himalaya and will facilitate future studies on the mechanism determining coexistence of animal species within complex system.

Key words: camera trapping, activity overlap, coexistence, hangul, Kashmir

Introduction

Information pertaining to how ecologically similar or sympatric species coexist is of paramount importance in understanding community diversity (Chesson 2000, HilleRisLambers et al. 2012). Intraguild competition plays an important role in shaping species' ecological niches by affecting their ability to access limited resources (Schmitt & Holbrook 1986, Case & Bolger 1991). Sympatric species often mitigate the negative impact of interspecific competition by partitioning resources along three main niche dimensions (time, food and space), resulting in niche differentiation (Schoener 1974a, b). Understanding the species' niche differentiation helps scientists and managers understand the capacity of species to coexist thereby benefitting conservation and management of ecological communities (HilleRisLambers et al. 2012).

In terms of time and space, spatially coexisting sympatric species conspicuously regulate their activity over a 24 h sleep-walk cycle, concentrating their peaks of activity to coincide with the hours of daylight, darkness or twilight and circadian rhythms leading to partitioning of resources structured among different sympatric species accordingly (Hayward & Slotow 2009). Terrestrial mammalian activity patterns can be categorized into diurnal (active during the day), nocturnal (active during darkness), crepuscular (active mostly during twilight) and cathemeral (active during hours of daylight and darkness) (Bennie et al. 2014). Though, activity patterns are highly variable among regions and across season, even within the same species but many factors affect activity patterns at local scale as well such as day length, temperature (Bennie et al. 2014), precipitation (HilleRisLambers et al. 2012), moonlight (Kotler et al. 2010, Kronfeld-Schor et al. 2013), prey-predator or competitive interactions (Schmitt & Holbrook 1986, Case & Bolger 1991, Johnsingh 1992, Linkie & Ridout 2011, Ramesh et al. 2012), and human activities (Carter et al. 2015). Such complex interactions obscure our understanding of the underlying processes governing activity patterns and selection pressures.

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In particular, we lack basic quantitative data on the details of activity patterns in sympatric mammal species. Activity patterns have been evaluated mainly through direct observation (Schaller 1967, Johnsingh 1983) or telemetry surveys of a limited number of individuals (Karanth & Sunquist 2000, Hussain 2013, Ensing et al. 2014), requiring high survey and capture efforts. In addition, disturbances caused by direct observation and live capture can bias the results or negatively affect animal populations. To overcome these challenges, camera-trap survey has received increasing attention during the last two decades mainly because it is cost effective, noninvasive to animals and produces information representing whole population in a given time frame. This survey method has been used to monitor the activity patterns of some mammal species in detail (van Schaik & Griffiths 1996, Azlan & Sharma 2006, Akbaba & Ayas 2012, Ramesh et al. 2012).

Another factor complicating any examination of species coexistence from activity periods is the degree of spatial overlap between the sympatric species. For instance, microhabitat differences in the distribution of species would allow coexistence of species that seemingly overlap in diet and activity. Therefore, sampling would include a measure of co-occurrence and account for the potential of significant differences in detectability between the species (MacKenzie et al. 2004).

In the Indian subcontinent, studies pertaining to coexistence and resource partitioning between predators considering space (e.g. Karanth & Sunquist 2000, Sankar & Johnsingh 2002, Andheria et al. 2007, Ramesh 2010) and time (e.g. Ramesh et al. 2012, Ross et al. 2013) have largely concentrated in the tropical forest ecosystems thereby leaving a void in understanding about other ecosystems. Little is known about the activity behaviour of mammals especially carnivores across the rugged Himalayan landscape owing to limited number of studies (e.g. Bashir et al. 2014, Carter et al 2015). The Jammu and Kashmir region has experienced political instability since 1948 due to border issues between India and Pakistan (Akbar 2002). Later on, with the eruption of insurgency in 1989 and increase in the military presence in the region, protection of wildlife became a low priority. Moreover, not even the declaration of protected areas in the region could facilitate conservation action and research on the status and distribution of several species in the region. Thus, the conservation and research took back seat (Bhatnagar et al. 2009) which led to creation of a knowledge gap (Mir et al. 2015).

In this study we examine patterns of co-occurrence, across the two axes of time and space, of eight species (comprising three strict carnivores, three omnivores and two herbivores) in a Himalayan moist-temperate forest of the Dachigam National Park, India, using camera traps and quantify spatio-temporal overlap among carnivores and their herbivorous prey. Our objectives were to: 1) determine the diel activity patterns of each species; 2) quantify the temporal patterns of overlap between species; and 3) measure the co-occurrence patterns between the species pairs. This information contributes to an understanding in a Himalayan moist-temperate forest comprising low prey abundances and should assist in developing more appropriate management and conservation strategies for forest communities in the mountainous regions.

Material and Methods

Study area

The Dachigam National Park (~141 km^2; 34°05′-34°12′ N, 74°54′-75°09′ E; 1650-4400 m a.s.l.) is one of the most important protected areas falling under the Northwest Himalayan biogeographic zone (2A) of India (Rodgers et al. 2000). The climate in Dachigam is sub-Mediterranean type with bi-xeric regime having two spells of dryness between April-June and September-November (Singh & Kachroo 1978). The area experiences irregular weather conditions with a considerable variation in the amount of precipitation. Snow is the main source of precipitation and in some higher parts melts by June. The park also serves as the catchment area for the famous Lake Dal and has received (during 2006-2013) an average annual rainfall of 734.9 mm (range = 577-1020 mm) (unpublished data). There is no definite rainy season, but four distinct seasons are recognised in the valley: winter (December-February), spring (March-May), summer (June-August) and autumn (September-November). The mean maximum temperature recorded during summer is 29.3 °C while the minimum during winter is –1.1 °C (unpublished data).

Administratively, the Dachigam National Park has been divided into the Lower Dachigam (~90 km^2) in the west and Upper Dachigam (~50 km^2) in the east (Naqash & Kumar 2011). The park holds the last viable population of hangul (~218 individuals, Charoo et al. 2011) which was formerly considered a subspecies of European red deer (*Cervus elaphus*) but recently given a new nomenclature *Cervus hanglu* ssp. *hanglu* Wagner, 1844 (Brook et al. 2017). The terrain in the park is rugged and steep criss-crossed by deep gorges, canyons and valleys. The series of

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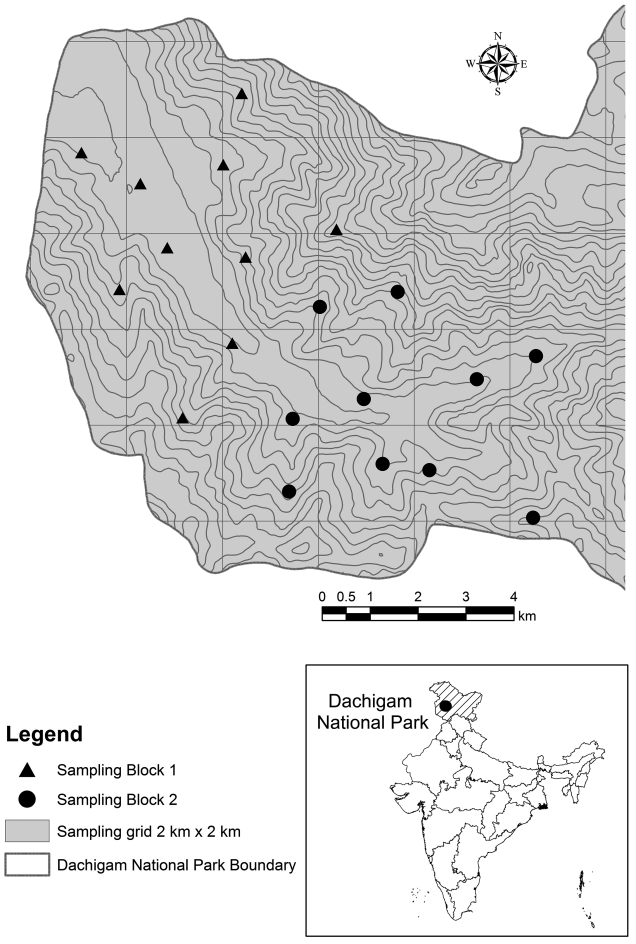


Fig. 1. Location of the camera traps in the sampling blocks in the study area (Lower Dachigam) Dachigam National Park, India.

undulations present a variety of slopes and aspects supporting an array of vegetation types which have been detailed elaborately elsewhere (see Singh & Kachroo 1978, Sharma et al. 2010) but broadly classified as Himalayan moist-temperate (Champion & Seth 1968). Other mammalian elements recorded in the park include Himalayan brown bear (*Ursus arctos* Linnaeus, 1758), Asiatic black bear (*Ursus thibetanus* Cuvier, 1823), leopard (*Panthera pardus* Linnaeus, 1758), red fox (*Vulpes vulpes* Linnaeus, 1758), Kashmir musk deer (*Moschus cupreus* Grubb, 1982), Himalayan serow (*Capricornis thar* Hodgson, 1831), Kashmir gray langur (*Semnopithecus ajax* Pocock, 1928), wild pig (*Sus scrofa* Linnaeus, 1758), yellow-throated marten (*Martes flavigula* Boddaert, 1785), jungle cat (*Felis chaus* Schreber, 1777), leopard cat (*Prionailurus bengalensis* Kerr, 1792) and Indian porcupine (*Hystrix indica* Kerr, 1792).

Camera Trapping

Data on activity patterns of the mammalian community was collected by means of camera trapping which was conducted during May-June, 2013 by dividing the area into a grid system of size 2 × 2 km (Fig. 1). Due to limited number of cameras (n = 20) available, a pair of cameras was put in each grid of 4 km^2. In total 20 grids were sampled for a period of 40 days (20 days each for two sampling blocks) generating an overall effective sampling effort of 396 trap nights, after subtracting the number of trap nights cameras were not functional. The camera trap locations were selected based on presence of carnivore sign, accessibility, terrain features, animal trails, nallahs (seasonal drainages) and an inter-camera distance of at least 1-2 km was maintained with a few exceptions because of constraints posed by the terrain. At each site, a pair of Cuddeback-attack™ digital cameras was set by affixing to trees at a height of approximately 30-45 cm to above the ground. The cameras were typically kept active for 24 h at a given location and set to take consecutive images (1 min picture interval) when triggered. Capture times for each species were assumed as a random sample of activity of the species, so that the likelihood of getting a photograph increases in proportion to how active the species is at that time of day. In order to maintain statistical independence and to reduce bias caused by repeat detections of the same animal, one record of each species per half an hour per camera site was considered as an independent detection and subsequent records were eliminated (O'Brien et al. 2003).

Diet activity patterns

Animal activity rhythms are known to match sun/moon related rhythms as circadian rhythms therefore, activity patterns can be understood to synchronise in accordance with the daylight and night hours (Kronfeld-Schor et al. 2013). Thus, animals can be broadly categorised into two main categories either nocturnal (active in night) or diurnal (active in day light), but some are active at the dawn and dusk, representing bimodal activity peaks or crepuscular pattern. Researchers (e.g. Weckel et al. 2006, Harmsen et al. 2011, Gerber et al. 2012, Ross et al. 2013) have arbitrarily defined the crepuscular time range (usually 1 to 1.5 h) band before and after local sunrise and sunset timings, respectively. Therefore, we define our crepuscular activity time bands according to local sunrise and sunset timings i.e. the civil twilight time at dawn and at dusk, respectively. According to Hut et al. (2013), in the Northern Hemisphere, ~80 % of the change of sunlight intensity takes place during the civil and nautical twilight timings. Civil twilight is defined as the time when the sun is between 6 and 0

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degrees below the horizon while the nautical twilight is defined as the time when the sun is between 12 and 6 degrees below the horizon. Therefore, we obtained the civil and nautical twilight times as well as the local sunrise and sunset timings from Thorsen (2008) and both the nautical and the civil twilights were used to categorize activity times. Thus, our crepuscular activity time band covers civil and nautical twilight times i.e. the whole time period when the sun is between 0 and 12 degrees below the horizon. The activity between local sunrise and sunset timings was considered as diurnal whereas the nocturnal activity was considered to be falling between astronomical twilight's (i.e. the time when the sun is between 18 and 12 degrees below the horizon) start in the evening till its end in the morning.

As discussed above, mostly animal activities are likely to be a function of light intensity and thus of the sun's position: time of sunrise and zenith or sunset. The clock time of sunrises, sunsets (hereafter sun time) differs according to the latitude, longitude and date of the year making patterns of behaviour to differ if analysed by clock time rather than by the deviation from sun time. Therefore, we standardized our observations by transforming the clock-recorded time of each detection to the relative sun time corresponding to the local sunrise and sunset times (Nouvellet et al. 2012).

We further examined species' selectivity to time periods by comparing use to availability of each time period (Manly et al. 2002). To see if species' activity was predominately classified as crepuscular, diurnal, or nocturnal, we calculated selection ratios of use to availability to each time period by each species following Manly et al. (2002): $w_i = o_i/p_i$

where w_i is the selection ratio for period i, o_i is the proportion of detections in period i and p_i is the elapsed time in period i as a proportion of total elapsed camera trap time. Elapsed times were calculated by summing over all camera trapping days and over all sites. Values of $w_i > 1$ indicate that the time period is selectively used more than availability whereas $w_i < 1$ indicates that the time period is avoided (Gerber et al. 2012). We used χ^2 tests to determine if species used the three time periods non-randomly. We regarded the detections in crepuscular, diurnal and nocturnal periods as a multinomial distribution and the probability in each class was determined by the length of that period. We calculated the length of periods as sum of all camera trapping days at all sites. Resource selection analysis was performed in program R (R Development Core Team 2016) using the "adehabitat" package (Calenge 2006).

Temporal overlap

We measured the overlap for all species pairs, using the coefficient of overlap, Δ, which ranges from 0 (no overlap) to 1 (complete overlap) to measure the extent of overlap between two kernel density estimates (i.e. daily activity patterns of two species compared) (Ridout & Linkie 2009). Overlap was defined as the area under the curve formed by taking the minimum of the two kernel density estimates at each point in time. Specifically, we used the overlap coefficient Δ_1 as recommended by Ridout & Linkie (2009) in cases of low sample sizes (Meredith & Ridout 2014). We used 1000 bootstrap samples to obtain percentile 95 % confidence interval (CI) of Δ_1 (Linkie & Ridout 2011). The calculated Δ_1 was compared between carnivores as well as between carnivores and potential prey species. Temporal overlap analyses were performed in program R (R Development Core Team 2016) using the "overlap" package (Meredith & Ridout 2014).

Species co-occurrence patterns

We tested the potential co-occurrence patterns between species pairs by using probabilistic models to test for statistically significant pairwise patterns of species co-occurrence (Veech 2013). This model allows one to calculate the probability (P) that two species co-occur at a frequency either less than (P_{lt}) or greater than (P_{gt}) the observed frequency of co-occurrence. The model is based on calculating P_j, the probability that two species co-occur at exactly j sites (sampled camera stations). Thus, if $P_{lt} < 0.05$, two species have a negative co-occurrence and if $P_{gt} < 0.05$ then there is positive co-occurrence between the two species. The probabilistic pairwise species co-occurence analysis was performed in program R (R Development Core Team 2016) using the "co-occur" package (Griffith et al. 2016).

Results

A total of ten species were recorded during the whole sampling period of 396 trap nights. Kashmir gray langur and wild pig had the fewest detections (n = 2 each) and therefore, were not considered for analysis. Table 1 summarises the remaining eight species that had variable detections amongst which red fox (n = 125) had the most detections while least number of detections (n = 13) was that of jungle cat.

Diet activity patterns

All the species except the Asiatic black bear, leopard and hangul exhibited non-random use of diurnal, nocturnal, and crepuscular periods (Table 1). The jungle cat, was detected more than expected during the

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Table 1. Number of detections n (selection ratio *w*) and the random use test of the diurnal, nocturnal and crepuscular periods given their availability by the mammals photo-captured during May-June 2013, in the Dachigam National Park, India.

Species	n (*w*) in time periods			Random use test (χ^2, df = 2)
	Diurnal	Nocturnal	Crepuscular	
Asiatic black bear	25 (0.919)	19 (0.983)	11 (1.297)	0.87, $P = 0.646$
leopard	7 (1.011)	3 (0.610)	4 (1.853)	2.12, $P = 0.345$
jungle cat	1 (0.156)	12 (2.627)	0 (0.000)	19.4, $P < 0.001$
leopard cat	2 (0.063)	43 (1.912)	19 (1.926)	69.61, $P < 0.001$
red fox	13 (0.210)	93 (2.118)	19 (0.986)	98.47, $P < 0.001$
yellow-throated marten	27 (2.022)	0 (0.000)	0 (0.000)	38.02, $P < 0.001$
Indian porcupine	1 (0.044)	39 (2.413)	6 (0.846)	60.45, $P < 0.001$
hangul	15 (1.011)	7 (0.664)	8 (1.730)	3.37, $P = 0.185$

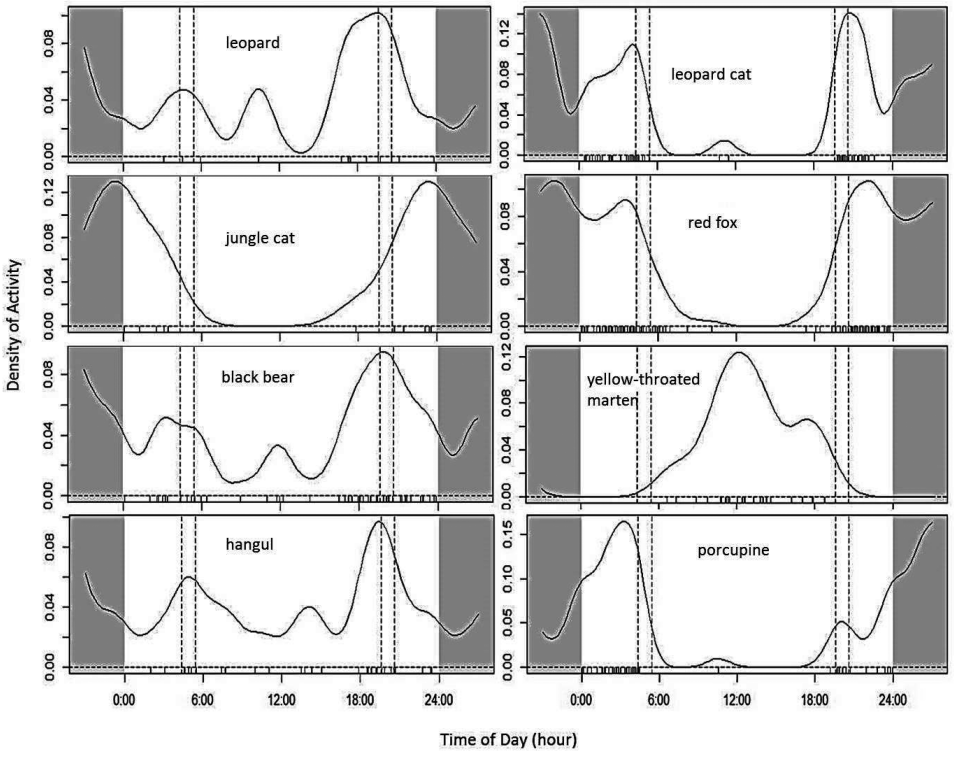


Fig. 2. Temporal activity patterns of the species recorded in Dachigam National Park during the study period. The four dotted vertical lines indicate start of nautical twilight, sunrise, sunset and end of nautical twilight, respectively.

nocturnal period ($P < 0.001$) and infrequently detected during the diurnal ($P = 0.000$) and crepuscular ($P = 0.000$) periods. The leopard cat was detected more than expected during the crepuscular ($P = 0.012$) and nocturnal ($P = 0.000$) periods and less than expected during the diurnal period ($P = 0.000$). Similarly, the red fox, we detected it more than expected during the nocturnal ($P = 0.000$) hours and less than expected during the crepuscular ($P = 0.947$) and diurnal ($P = 0.000$) periods. Yellow-throated marten was detected during the diurnal hours ($P = 0.000$) only with not a single detection during the crepuscular and nocturnal periods. For the Indian porcupine, we detected it mostly during the nocturnal hours ($P = 0.000$) while detecting it infrequently during the crepuscular ($P = 0.633$) and diurnal ($P = 0.000$) hours.

Temporal overlap

Daily activity patterns of six carnivore species detected in the study area are presented in Fig. 2. Highest overlap was found between Asiatic black bear and hangul with an overlap coefficient, $\Delta_1 = 0.81$ followed by leopard and hangul ($\Delta_1 = 0.79$). On the other hand, least overlap ($\Delta_1 = 0.47$) was found between hangul and yellow-

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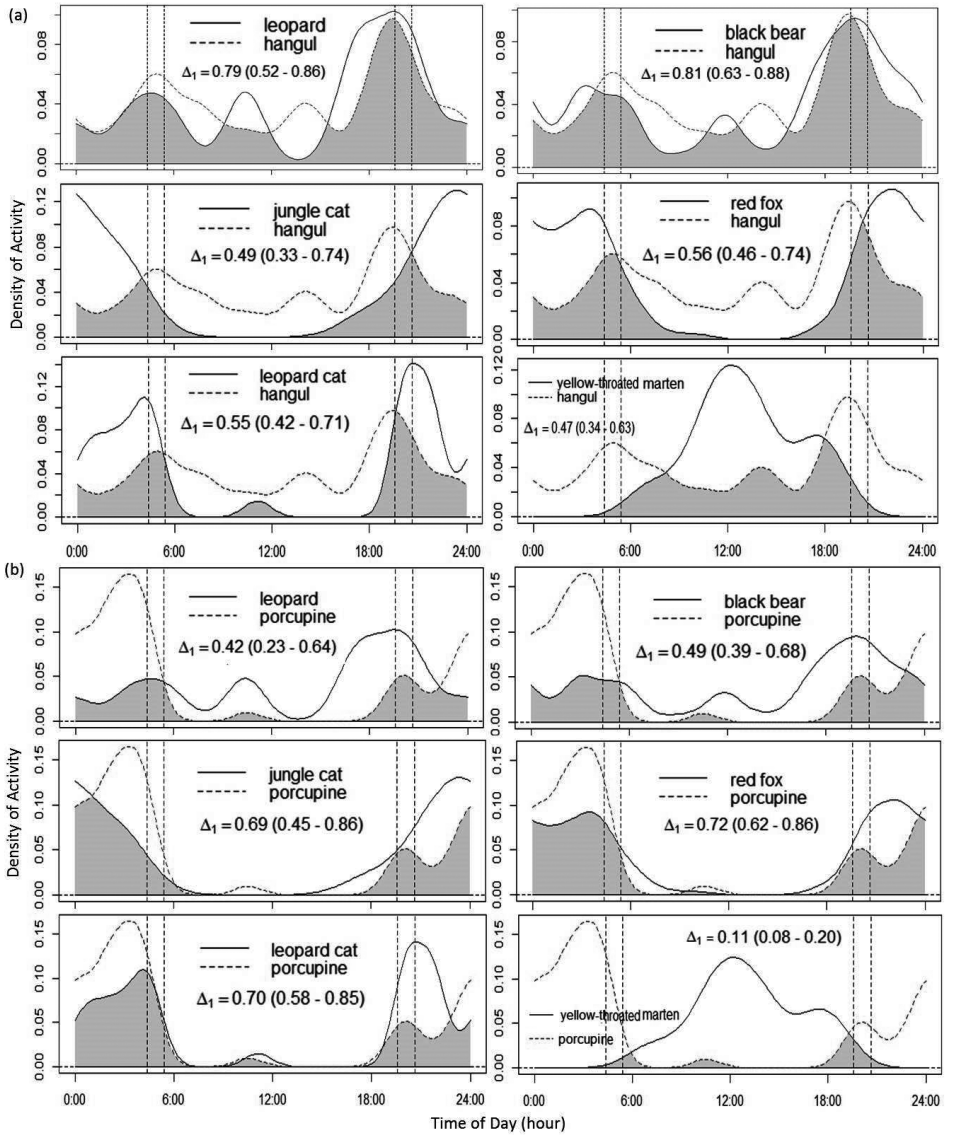


Fig. 3. Temporal overlap (shaded area) between six carnivore species and herbivore species (a) hangul and (b) Indian porcupine considered as prey. Coefficient of overlap (Δ_1) given for each pair along with percentile 95%CI given in parentheses. The four dotted vertical lines indicate start of nautical twilight, sunrise, sunset and end of nautical twilight, respectively.

throated marten (Fig. 3a). Similarly, highest coefficient value was for red fox and Indian porcupine temporal overlap ($\Delta_1 = 0.72$), followed by leopard cat and Indian porcupine ($\Delta_1 = 0.70$, Fig. 3b). Amongst carnivore species, highest temporal overlap was found between leopard and Asiatic black bear ($\Delta_1 = 0.84$), followed by red fox and jungle cat ($\Delta_1 = 0.82$), whereas the least overlap among carnivores was between yellow-throated marten and leopard cat ($\Delta_1 = 0.12$, Table 2).

Species co-occurrence patterns

The results (Table 2) from the probabilistic pairwise co-occurrence analysis suggest that 25 of the 28 total classifiable species pairs were "truly random" associations as none of the 25 species pairs exhibited significantly negative or positive co-occurrence patterns at the study sites ($P_{lt} > 0.05$, $P_{gt} > 0.05$). The significant non-random associations which were positive were only two in which hangul exhibited significantly positive co-occurrence patterns with the leopard cat ($P_{gt} = 0.012$) and the Indian porcupine ($P_{gt} = 0.039$). The remaining species pair (Indian porcupine and leopard cat) was deemed unclassifiable ($P_{lt} > 0.05$, $P_{gt} = 0.052$).

Discussion

This study provides first information pertaining to coexistence in mammalian community of the moist-temperate forest of the Kashmir Himalaya, India, however with sample size limitations. Although we

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Table 2. Temporal overlaps and species co-occurrence patterns between the species pairs. Temporal overlaps (upper half of the table in light gray) between the species pairs with overlap coefficient values (Δ_1) given on top and below are the percentile 95 % confidence intervals given in parentheses. The species are sorted from highly carnivorous (leopard/leopard cat) to herbivorous (Indian porcupine). High temporal overlaps ($\Delta_1 >$ 0.75) are bold. The lower half of the table (dark gray) presents standardized effect sizes (differences between expected and observed frequency of co-occurrence) for easy comparisons among studies and methods (Griffith et al. 2016). These standardized values are bounded from −1 to 1, with positive values indicating positive associations and negative values indicate negative associations. Statistically significant values are bold ($P_{lt} < 0.05$ or $P_{gt} < 0.05$).

	leopard cat	jungle cat	red fox	Asiatic black bear	yellow-throated marten	hangul	Indian porcupine	
	0.55 (0.34-0.72)	0.49 (0.25-0.74)	0.55 (0.33-0.74)	**0.84** (0.54-0.86)	0.46 (0.27-0.67)	**0.79** (0.52-0.86)	0.42 (0.23-0.64)	leopard
jungle cat	0.040	0.70 (0.52-0.86)	**0.83** (0.72-0.91)	0.63 (0.54-0.77)	0.12 (0.11-0.21)	0.55 (0.42-0.71)	0.70 (0.58-0.85)	leopard cat
red fox	0.060	0.050	**0.82** (0.60-0.91)	0.60 (0.41-0.78)	0.15 (0.06-0.34)	0.49 (0.33-0.74)	0.69 (0.45-0.86)	jungle cat
Asiatic black bear	0.060	0.000	–0.010	0.66 (0.54-0.78)	0.15 (0.14-0.23)	0.56 (0.46-0.74)	0.72 (0.62-0.86)	red fox
yellow-throated marten	0.025	0.060	0.040	–0.010	0.40 (0.30-0.58)	**0.81** (0.63-0.88)	0.49 (0.39-0.68)	Asiatic black bear
hangul	**0.140**	0.010	0.070	0.020	0.060	0.47 (0.34-0.63)	0.11 (0.08-0.20)	yellow-throated marten
Indian porcupine	0.110	0.050	0.090	–0.010	–0.010	**0.120**	0.45 (0.33-0.64)	hangul
leopard	0.055	0.040	0.080	0.080	–0.005	0.000	0.030	

initially aimed to collect data on leopard for longer periods covering seasons but constraints like limited number of cameras and security concerns hampered the overall sampling duration. Other sympatric mammals such as the "endangered" Kashmir gray langur and wild pig (which reappeared after a long gap of 30 years during the sampling period, Khursheed et al. 2013) were also recorded but could not be included in the analysis due to very low detections. In rugged terrain of the mountainous regions, camera trap survey seems more cost-efficient, in terms of both finance and human effort, than other survey methods, and provides very detailed biological information on diel activity patterns.

Diet activity patterns and temporal overlap

The large mammals in this study are found to be active both day and night indicating no clear cut selection from the three diel categories and thus, can be understood to have cathemeral pattern of activity. This could be attributed, at least partially, to the energy requirements imposed by their large body sizes which require being active more time (van Schaik & Griffiths 1996). We explore plausible justifications pertaining to this behaviour in each case of the three species. In case of hangul, it showed firstly, two distinct activity peaks in the twilights around dawn and dusk which is consistent with studies conducted in the temperate ecosystems (Georgii & Schröder 1983, Boyce et al. 2010, Ensing et al. 2014). Second, we assume that hangul (as ~73 % were females) has more energy requirements during the sampling period, which marks the onset of the fawning (Prater 1980), due to which it is compelled to remain active during daylight hours. Finally and most importantly, it has to trade-off, by remaining active 24 h period, between minimizing predation risk while maximising the food intake to supplement energy requirements and this is in agreement with what has been reported by Ensing et al. (2014). On the other hand, it is well known that some predators such as cats hunt primarily by auditory and visual cues (Sunquist & Sunquist 2002) and therefore, synchronise their activities in accordance with the activity pattern of their prey species. This is the case of leopard which in forested ecosystems has a diurnal activity pattern matching with that of prey activity (Jenny & Zuberbuhler 2005). Leopard activity pattern is similar to that of hangul in our study at least for the sampling duration when pregnant hangul females are more susceptible to get killed. Our study on ecological aspects of leopard in the Dachigam National Park has revealed that this area has very poor prey base which costs leopard very high searching efforts (e.g. largest home ranges sizes, data not presented here) and

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very low benefits (Habib et al. 2014). This prey scarcity ultimately forces the leopard to spend great amount of energy in search efforts across time and space thus, resulting cathemeral activity. In case of Asiatic black bear, it is also diurnally active throughout the summer in the study area (Prater 1980) so as to compensate for the energy lost during the previous winter season. It has to spend most of its time in search of food under a very high competition with conspecifics (for vegetal food/and animal matter) as well as other carnivores (for animal matter), since the study area harbours very high Asiatic black bear densities; 1.3-1.8 bears/km^2 (Saberwal 1989), 48/100 km^2 (Sathyakumar et al. 2013).

This study finds the two small cats (leopard cat and jungle cat) to be primarily nocturnal which is consistent with other reported studies only in case of leopard cat (Prater 1980, Grassman 2000, Lynam et al. 2013, Mukherjee 2013), nevertheless there are studies contradicting nocturnality of leopard cats (Rabinowitz 1990, Azlan & Sharma 2006, Austin et al. 2007). According to Prater (1980), jungle cat is diurnal as well as crepuscular and can even kill Indian porcupines which are nocturnal. We found jungle cat to be strictly nocturnal as reported by Majumder et al. (2011). According to several studies (Harmsen et al. 2011, Bashir et al. 2014) the daily activity of many felids is correlated with the activity pattern of their prey. The main reason of these small cats being nocturnal in the study area could be that rodents, their main prey, are generally nocturnal (Prater 1980, Bashir et al. 2014) although we could not quantify this point through camera trapping.

The only canid species recorded during this study was red fox. Most of the studies indicate that the red fox is a generalist predator that uses resources according to their availability and hence is opportunistic in its behaviour (Webbon et al. 2006, Dell'Arte et al. 2007). According to Nowak (1999), it has nocturnal and crepuscular activity behaviour which our results also confirm. Like the two small felids, the red fox too predominantly depends on rodents in this study area (~50 %, Bora 2012). The yellow-throated marten was completely a diurnal species in the study area and has been suggested as "primarily diurnal" by Nowak (1999), but can hunt both by day and night (Prater 1980). It is also known to attack young deer (Prater 1980) due to which its predation potential on hangul fawns can be anticipated during the sampling period, at least, which coincides with the onset of hangul fawning (Prater 1980). On the other hand, Indian porcupine is mainly a nocturnal species with little activity during the twilight (crepuscular). The Indian porcupine has been described as a nocturnal species (Menon 2014).

The activity timings varied amongst different sympatric carnivore species in our study area. Among large carnivores, leopard was active almost equally during light and dark (night and crepuscular hours) periods of the day. Our results show that activity patterns of both leopard and Asiatic black bear match with hangul activity resulting in very high values of temporal overlap coefficients (Table 2 and Fig. 3).

Species co-occurrence

We found no statistically significant spatial co-occurrence patterns between the species pairs. Except for the two pairs (hangul/leopard cat and hangul/Indian porcupine) which were positively associated, all other 26 pairs analysed were random i.e. no positive or negative associations shown. Therefore, the spatial niche differentiation among the species in the study area is not a determining factor in the area. The species have to differentiate on other two dimensions of niche i.e. time and diet. In case of time the species pairs which had high temporal overlap also had difference on their general diet patterns (carnivore, omnivore or herbivore) (Table 2). Thus, we can assume that species co-occurrence in the study area may be maintained by partitioning the ecological niches or resources at a finer scale; therefore, further studies are needed to determine factors controlling their co-occurrence and potential interactions at a micro-scale.

We recognise drawbacks of small data sets for some species and short span of time but owing to the importance of the species and the ecosystem, every bit of information is crucial for the management which should be interpreted with caution. Moreover, according to Ramesh et al. (2012), camera traps are effective in recording spatio-temporal patterns with certain limitations in their use, like the inability to account for detection probability, which is bound to vary with species. Since, cameras are placed along trails and roads keeping in mind the large carnivores, this bias may affect the ungulate capture rates (Ramesh et al. 2012). This ecosystem consists an unbalanced number of species comprising several small to large predators and an important ungulate species hangul which is numerically small in population (~218 odd individuals, Charoo et al. 2011) and high conservation status (Mukesh et al. 2015). Moreover, there are other ungulate species with unknown population status owing to their very low abundance, thus, further studies are needed in order to explicitly understand the coexistence patterns within these communities.

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