



Patterns of species co-occurrence in a diverse Eastern Himalayan montane carnivore community

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Abstract

We investigated patterns of species richness and co-occurrence in a montane carnivore community within a forested landscape in Bhutan that ranged in altitude from 2000 to 3760 m above sea level, and covered an area of approximately 140 km². Species were detected by unbaited camera traps set along animal trails and baited camera traps set away from trails. During the 6-month study, we gathered 1,329 independent mammal events from 67 camera-trap locations, of which, 145 (10.9%) were of 13 different carnivore species from five different families. Four carnivores were IUCN red-listed threatened species: tiger (*Panthera tigris*), marbled cat (*Pardofelis marmorata*), dhole (*Cuon alpinus*), and Asiatic black bear (*Ursus thibetanus*). For most camera stations where carnivores were detected, only a single carnivore species was captured on camera and there was evidence of temporal partitioning of activity between large (tiger and leopard, *Panthera pardus*) and small (marbled cat, golden cat *Catopuma temminckii*, and leopard cat *Prionailurus bengalensis*) felids, and between two common mustelids, the Siberian weasel (*Mustela sibirica*) and yellow-throated marten (*Martes flavigula*). Furthermore, we detected significant non-random spatial co-occurrence for most pairwise comparisons of carnivores despite the short timeframe of our study. This, combined with temporal patterns in activity, facilitates localized species co-occurrence in a diverse montane carnivore community.

Keywords Bhutan · Biological corridors · Carnivore communities · Mammal · Mesocarnivore · Species richness

Introduction

Carnivores are important members of most mammal communities and despite existing at naturally low densities, can often exert strong influence on other species in the community. Mammalian carnivores tend to exert top-down influence on herbivores through direct predation (Andersen et al. 2006) with profound effects on the flow of nutrients and the

structure of food webs (Ripple et al. 2014; Roemer et al. 2009). Large carnivores exert further population pressure on smaller mesocarnivores through intraguild competition (Ripple et al. 2014) encompassing direct predation (Mohammadi et al. 2017; Palomares and Caro 1999), or influencing changes in mesocarnivore behavior and resource use to avoid antagonistic interactions (Thinley et al. 2018). Avoidance mechanisms include using different habitat types (Ramesh et al. 2017; Schaller 1967; Steinmetz et al. 2013), having different activity schedules (Steinmetz et al. 2013), and utilizing fine-scale movement patterns (Ramesh et al. 2017) to achieve avoidance in a shared environment. Avoidance mechanisms are not mutually exclusive. For example, Steinmetz et al. (2013) showed that the common leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) spatially avoided habitats with tigers (*Panthera tigris*), and were active at times that tigers were not. Similarly, Ramesh et al. (2017) showed that common leopards used temporal means to avoid lions (*Panthera leo*), but spatial means to avoid hyenas (*Crocuta crocuta*).

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Carnivores reach their highest richness in two global biogeographical regions: the Afrotropical Region of sub-Saharan Africa and the Indo-Malaysian Region extending from insular South East Asia to the Eastern Himalayas (Crooks et al. 2008; Procheş and Ramdhani 2012). Here, carnivore communities are typically dominated by the families Felidae, Canidae, Mustelidae, and Viverridae (Chutipong et al. 2017; Kauffman et al. 2007; Kawanishi and Sunquist 2004; Schuette et al. 2013). Although regional and global patterns of mammal diversity in Asia are relatively well understood (Chi et al. 2020; Dorji et al. 2018), local patterns of species richness and community structure remain poorly known due to costly field surveys, difficulty in detecting uncommon or cryptic species, and difficulty distinguishing species from indirect signs like pug-marks and scats (Sangay et al. 2014). However, rapid advancement of heat-in-motion camera trap technology has revolutionized wildlife ecology (Meek et al. 2015) with some camera trap studies in Asia revealing localized carnivore community richness comparable to broader regional scales, with as many as 18–20 co-occurring carnivore species detected within relatively small areas (Chutipong et al. 2017; Johnson et al. 2006; Kawanishi and Sunquist 2004). Camera traps also represent a non-invasive method of gathering spatiotemporal data on animals, even when they occur at low densities (Karanth et al. 2017).

Bhutan, situated in the Eastern Himalayas at the intersection of the Palearctic and Indo-Malaysian biogeographical regions (Procheş and Ramdhani 2012), has an altitudinal range encompassing a diversity of habitats from low-altitude tropical rainforest, mid-altitude broadleaf and mixed conifer forest, to high-altitude alpine and scree (Tharchen 2013). Correspondingly, Bhutan has a rich mammal diversity that includes at least 39 species of carnivores (Wangchuk et al. 2004), contributing to its listing as a global biodiversity hotspot (Mittermeier et al. 2011). Localized carnivore richness is also high. For example, a camera-trapping study by Tempa et al. (2013) in the tropical lowlands of Royal Manas National Park revealed 16 co-occurring carnivore species, including six felid species. However, little information exists on carnivore diversity in mid-to high-altitude forests in Bhutan.

Both large and small Asian carnivores are highly threatened by habitat destruction, agricultural expansion, over-hunting, and poaching (Ashrafzadeh et al. 2020; Marneweck et al. 2021). This is especially evident in the Eastern Himalayas (Dorji et al. 2018) with its high rates of deforestation and habitat fragmentation (Pandit et al. 2007) in conjunction with high hunting pressure (Velho et al. 2012) and a high human population density (Mittermeier et al. 2011). Such substantial anthropogenic pressure necessitates a better understanding of Asian carnivore community ecology for conservation planning (Dalerum et al. 2009). In particular, Marneweck et al. (2021) recently encouraged the need

for more research on the ecology and demography of small Asian carnivores to inform conservation, given current and future threats from global change. Our investigation on carnivore co-occurrence in a montane zone of central Bhutan in the Eastern Himalayas addresses this premise toward conserving threatened carnivores, and supplements the lack of information on carnivore community richness at this elevation zone.

Materials and methods

Study area

We undertook a camera trap mammal survey over 6 months between November 2012 and April 2013 in Corridor 8 of Bhutan's Biological Corridor Complex (Fig. 1), which connects Jigme Singye National Park in central Bhutan with Wangchuk Centennial and Jigme Dorji National Parks in the north of the country. Our study area covered approximately 140 km² ranging in altitude from 2000 to 3760 m above sea level (asl). Lower elevation (2000–2700 m asl) zones comprised cool broadleaf forest; mid-elevation (2700–3500 m asl) zones were either cool broadleaf forest or mixed conifer forest (including spruce *Picea spinulosa*, hemlock *Tsuga dumosa*, Blue pine *Pinus wallichiana*, and larch *Larix* spp.); and high-elevation zones (above 3500 m asl) were sub-alpine forest that was either pure stands of fir (*Abies densa*) with a bamboo dominated understorey, or a mix of species including various conifers, juniper (*Juniperus recurva*), and rhododendron (*Rhododendron* spp.). Habitat across the study area was generally intact and only moderately impacted by some cattle grazing, and sustainable collection of firewood, timber, and non-wood forest products by local people. Narrow footpaths used by people, livestock, and wildlife traversed most spurs and ridgelines, while small grazing meadows and livestock herder huts dotted the predominantly forested landscape. The east–west National Highway (at the time a narrow single-lane road) bisected the corridor.

Survey methods

We surveyed 16 × 1000-m-long transects along footpaths and game trails, with a random starting point for each transect. Starting at 0 m along each transect, we established a 50 × 50-m survey plot at 500-m intervals that was placed 100 m away from each transect along a randomly generated compass heading. We recorded all signs of vertebrate fauna (both direct sightings and indirect evidence) in the plot. We additionally undertook a detailed vegetation survey in a nested 20 × 20-m subplot. A Reconyx Hyperfire PC850 white-flash camera trap, set to take 5 photos per trigger with no “quiet time,” was placed at the center of

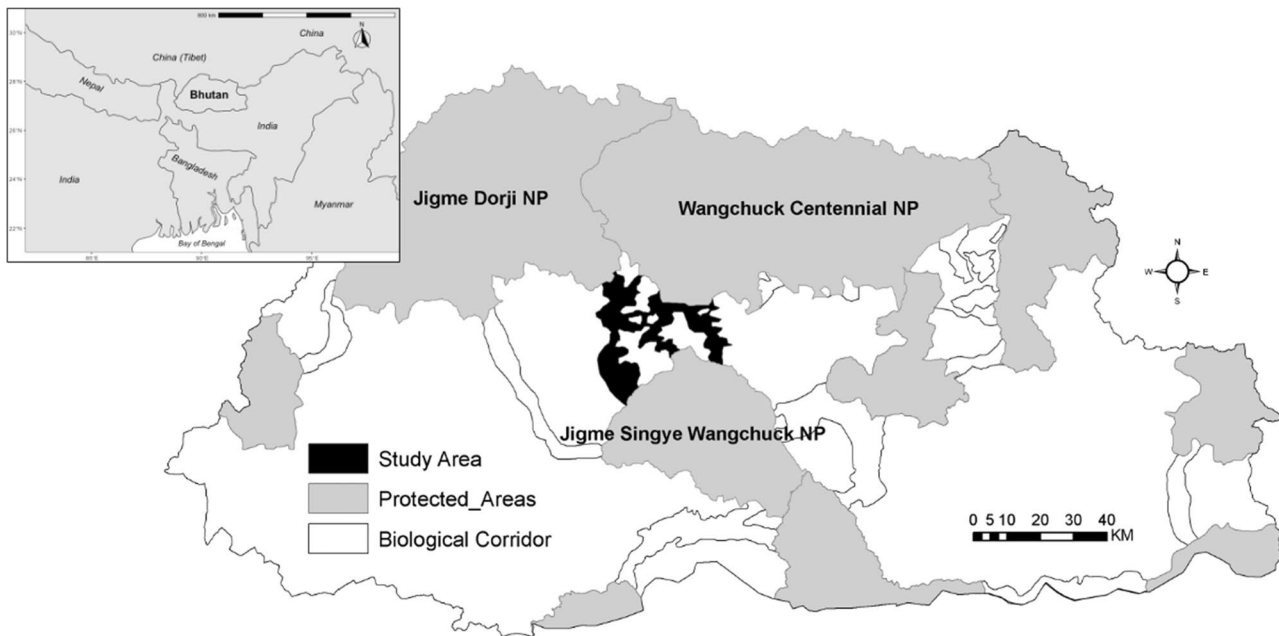


Fig. 1 The study area in central Bhutan. This corridor, known as “Corridor 8” in the Bhutan Biological Corridors Complex (B2C2), links Jigme Singye Wangchuck National Park in the south to Jigme

Dorji National Park and Wangchuck Centennial National Park in the north. Outlines of other corridors in the B2C2 and their relationship to protected areas, is also indicated

each survey plot and positioned 30 cm from the ground and 1.5 m from a bait canister containing cotton wool soaked in truffle oil as a lure. These cameras, hereafter referred to as “plot cameras,” aimed to capture carnivores that avoided main trails. We set Cuddeback Attack white-flash camera traps on the main transect (trail) at intervals not less than 100 m from one another, to detect carnivore species using the trail. These camera traps (hereafter called “trail cameras”) were not baited, and their deployed locations were non-random and selected on the evidence of pronounced mammal activity (scats, tracks, scrapes, etc.) most notably at the convergence of two or more game trails and/or forest paths. We affixed trail camera traps to tree trunks at a height of approximately 0.5–1 m. These camera traps faced the main trail at an angle of approximately 45° relative to the direction of the trail. Camera traps ran for 36–51 days (average \pm S.D. = 43 ± 5 days) before being recovered and redeployed at new transects. In total, we set 40 plot cameras (20 in cool broadleaf forest, 15 in mixed conifer forest, and five in sub-alpine forest) and 27 trail cameras (14 in cool broadleaf forest, seven in mixed conifer forest, and six in sub-alpine forest) for a total of 3,085 trap days and nights.

We sorted photos of carnivore species at each camera location and processed them using the “CameraSweet” camera trapping analysis software (Sanderson and Harris 2013). We considered independent events to be those where 30 or more minutes had elapsed between successive photos of the same species at the same camera. A similar 30-min cut-point

for independent events has been commonly used in other carnivore studies (Dorji et al. 2019; Edwards et al. 2015; Kennedy et al. 2018; Vernes et al. 2015).

Analytical methods

For carnivore species with adequate number of records for meaningful comparisons (tiger, leopard, golden cat *Catopuma temminckii*, leopard cat *Prionailurus bengalensis*, Asiatic black bear *Ursus thibetanus*, dhole, Siberian weasel *Mustela sibirica*, and yellow-throated marten *Martes flavigula*), we investigated carnivore assemblage structure at our 67 camera trap stations by examining pairwise relationships between species using the probabilistic model of species co-occurrence developed by Veech (2013) within the R package “cooccur” (Griffith et al. 2016). We assumed potential avoidance between species based on inter-specific competition for resources, i.e., leopard cat avoiding golden cat (Rasphone et al. 2020) and Siberian weasel avoiding yellow-throated marten (Zhao et al. 2020), or antagonistic interactions such as leopard and dhole avoiding tiger (Seidensticker 1976; Steinmetz et al. 2013; Thinley et al. 2018), dhole avoiding leopard (Karanth et al. 2017), and Siberian weasel avoiding yellow-throated marten (Zhao et al. 2020). We tested these interactions explicitly for subsets of camera data that detected these species, rather than examining all possible pairwise combinations. Prior to analyses, we created a “site mask” (see Griffith et al. 2016) to exclude sites at which

particular mammal species would not be expected to occur based upon the elevational range for each species. Information on elevation ranges was drawn from a nation-wide wildlife camera trapping dataset (Sangay et al. 2019) which yielded minimum and maximum elevation recorded for each species in our study area. That dataset comprised approximately 10 million photographs obtained from 148,598 trap-nights across 1858 camera traps deployed within 1129 5-km × 5-km grids across Bhutan.

Results

Sampling effort

During our 6-month survey, we gathered approximately 16,000 images from 67 camera-trap locations (40 plot cameras; 27 trail cameras) and recorded 1,329 independent mammal events from these images, of which, 145 (10.9%) were carnivore species. Carnivores were detected at 44 (65.7%) of the 67 camera traps. There was no significance difference in carnivore detections between plot (61 detections; 42.4%) and trail (83 detections; 57.6%) cameras ($t = 1.02$; $df = 12$; $p < 0.5$), although some species were more likely to occur at one type of camera station over the other. For example, dhole were only detected on trail cameras (n events = 16) while Siberian weasels were mostly detected on plot cameras (n events = 15) compared to trail cameras (n events = 5).

Species richness

We detected thirteen species of mammalian carnivores from five families (Table 1). Families comprised Felidae (5 species), Canidae (2 species), Ursidae (1 species), Mustelidae (3 species), and Viverridae (2 species). Four were IUCN red-listed threatened species: tiger (endangered; 7 records), dhole (endangered; 16 records), common leopard (vulnerable; 12 records), and Asiatic black bear (vulnerable; 23 records) (Table 1). Two additional cat species (marbled cat *Pardofelis marmorata*; 4 records and Asiatic golden cat; 13 records) are listed as near-threatened by the IUCN (Table 1).

We detected the yellow-throated marten at the highest number of camera trap sites (15 sites; 22% of total) followed equally by the Siberian weasel and Asiatic black bear (12 sites; 18% of total), and then the leopard cat (10 sites; 15% of total). Three species (Himalayan palm civet *Paguma larvata*; spotted linsang *Prionodon pardicolor*; and yellow-bellied weasel *Mustela kathiah*) were each detected at a single site, and only once (Table 1). Fifty percent ($n = 22$) of our camera traps detected only a single carnivore species while 22.7% ($n = 10$) and 18.2% ($n = 8$) detected two and three species, respectively. Only 4.5% ($n = 2$) of camera traps detected the presence of ≥ 4 carnivore species.

Temporal and spatial partitioning

Most pairwise comparisons had co-occurrences which were significantly different from the expected co-occurrence (Table 2). Strongest differences were found among the small carnivores. For species that occurred at more than four cameras (Asiatic golden cat, leopard cat, Siberian weasel, and yellow-throated marten), all pairwise comparisons returned co-occurrences which were significantly lower than would be expected by chance (Table 2). For large carnivores, significant negative co-occurrences were detected between Asiatic black bear and tiger, Asiatic black bear and dhole, tiger and dhole, and common leopard and dhole, but not between tiger and common leopard, or Asiatic black bear and common leopard (Table 2).

Tigers exhibited strong diurnal activity overlap with leopards (55% overlap; Fig. 2a) and dholes (74% overlap; Fig. 2b). For other carnivore species with sufficient activity data, yellow-throated martens were strongly diurnal with activity peaking at mid-afternoon whereas Siberian weasels were primarily nocturnal, but with activity peaks that extended from early evening through to mid-morning (40% overlap; Fig. 2c). Despite a 45% activity overlap, Asiatic golden cats were predominantly diurnal compared to leopard cats (Fig. 2d).

When differentiated by size, there was evidence of temporal activity partitioning between the large felid and canid guild (tiger, leopard, dhole) and the small felid (marbled, golden, and leopard cats) guild despite a 46% overlap (Fig. 2e). Large predators were more diurnal than small felids with their activity being broadly crepuscular, while small felids were predominantly nocturnal. Asiatic black bears exhibited both diurnal and nocturnal behaviors with a 60% overlap with the large felid and canid guild (Fig. 2f).

Despite being present across all forest types, most carnivore species were associated with a particular forest type and elevation range (Fig. 3). For example, Asiatic black bears were most common in low-elevation cool broadleaf forest (2000–2700 m; Fig. 3a) whereas dhole mostly occurred in mid-elevation cool broadleaf forest (2700–3500 m) and high-elevation alpine habitat (> 3500 m; Fig. 3b). Tiger and common leopard largely occupied separate forest types. Leopards were found mostly in low-elevation cool broadleaf forest (Fig. 3c) at elevations < 2800 m whereas tigers were common to mid-elevation mixed conifer forest and high-elevation alpine habitat (Fig. 3d) up to 3760 m. Leopard cats and yellow-throated martens were mostly found in low-elevation cool broadleaf forest (Fig. 3f, g) whereas Siberian weasels were found at high-elevation mixed conifer forest and alpine habitat (Fig. 3h).

Table 1 Species of carnivore detected during 3,085 camera-trap days and nights in central Bhutan

Common name	Species	IUCN status ^a	Max body weight (kg) ^b	Independent cameras ^c	Independent events—trail	Independent events—plot cameras ^c	NUMBER OF CAMERA SITES	% of all mammal events
Felidae								
Tiger	<i>Panthera tigris</i>	EN	260	6	1	6	6	0.57
Common leopard	<i>Panthera pardus</i>	VU	90	4	8	4	6	0.97
Asiatic golden cat	<i>Catopuma temminckii</i>	NT	15	8	5	8	8	1.05
Leopard cat	<i>Prionailurus bengalensis</i>	LC	7	16	8	16	10	1.95
Marbled cat	<i>Pardofelis marmorata</i>	NT	5	2	2	2	4	0.32
Canidae								
Dhole	<i>Cuon alpinus</i>	EN	21	16	0	16	7	1.30
Red fox	<i>Vulpes vulpes</i>	LC	10	2	0	2	1	0.16
Ursidae								
Asiatic black bear	<i>Ursus thibetanus</i>	VU	110	14	9	14	12	1.87
Mustelidae								
Yellow-throated marten	<i>Martes flavigula</i>	LC	3	10	11	10	15	1.70
Yellow-bellied weasel	<i>Mustela kathiah</i>	LC	1.5	0	1	0	1	0.08
Siberian weasel	<i>Mustela sibirica</i>	LC	0.8	5	15	5	12	1.62
Viverridae								
Himalayan palm civet	<i>Paguma larvata</i>	LC	5	0	1	0	1	0.08
Spotted linsang	<i>Prionodon pardicolor</i>	LC	0.7	1	0	1	1	0.08
All carnivores				84	61	84	44	10.9

^aEN endangered, VU vulnerable, NT near threatened, LC least concern

^bFrom Nowak (1999)

^c“Plot cameras” were set at the center of survey plots away from trails; “trail cameras” were cameras set on a forest path or game trails (see the “Methods” section for details)

Table 2 Observed and expected frequencies of co-occurrence between species pairs. For each pair, the probability indicates whether a lower value of co-occurrence than the expected value, could have

been obtained by chance. Thus, P -values < 0.05 indicate a significant difference between observed and expected values

Pairwise comparison	N Sites with species (1)	N Sites with species (2)	Observed co-occurrence	Expected co-occurrence	Probability
Large carnivores					
(1) Asiatic black bear, (2) tiger	11	6	2	4.4	$P < 0.05$
(1) Asiatic black bear, (2) dhole	11	7	3	5.1	$P < 0.05$
(1) Asiatic black bear, (2) common leopard	11	6	3	4.7	NS
(1) Tiger, (2) dhole	6	6	1	3.3	$P < 0.05$
(1) Tiger, (2) common leopard	6	3	1	2.2	NS
(1) Common leopard, (2) dhole	6	5	1	3.5	$P < 0.01$
Small carnivores					
(1) Asiatic golden cat, (2) leopard cat	7	10	1	4.4	$P < 0.001$
(1) Leopard cat, (2) Siberian weasel	10	10	0	5	$P < 0.0001$
(1) Leopard cat, (2) yellow-throated marten	10	14	2	6.4	$P < 0.001$
(1) Siberian weasel, (2) yellow-throated marten	12	15	3	7.5	$P < 0.001$

Discussion

Species richness

The Eastern Himalayan region supports rich carnivore diversity at regional scales (Dorji et al. 2018) and camera trapping (Bu et al. 2016; Johnson et al. 2009) has revealed high species richness at local scales. Although our study timeframe was short and within a relatively small study area (140 km²), we successfully detected the presence of 13 co-occurring carnivore species. Another carnivore, the red panda (*Ailurus fulgens*), has since been detected by us (unpublished data) in the same study area as part of ongoing work. Although some camera trapping studies in the Eastern Himalayas have reported local site-specific carnivore richness as high as 16 species (Datta et al. 2008; Naniwadekar et al. 2013; Tempa et al. 2013), these studies focused on the species-rich tropical lowland forest. Our study indicates that local carnivore richness in mid- to high-elevation (2000–3760 m) montane forests of the Eastern Himalayas is comparable to that found in the region's tropical lowlands, demonstrating that these montane forests are equally important landscapes in supporting a diverse carnivore community.

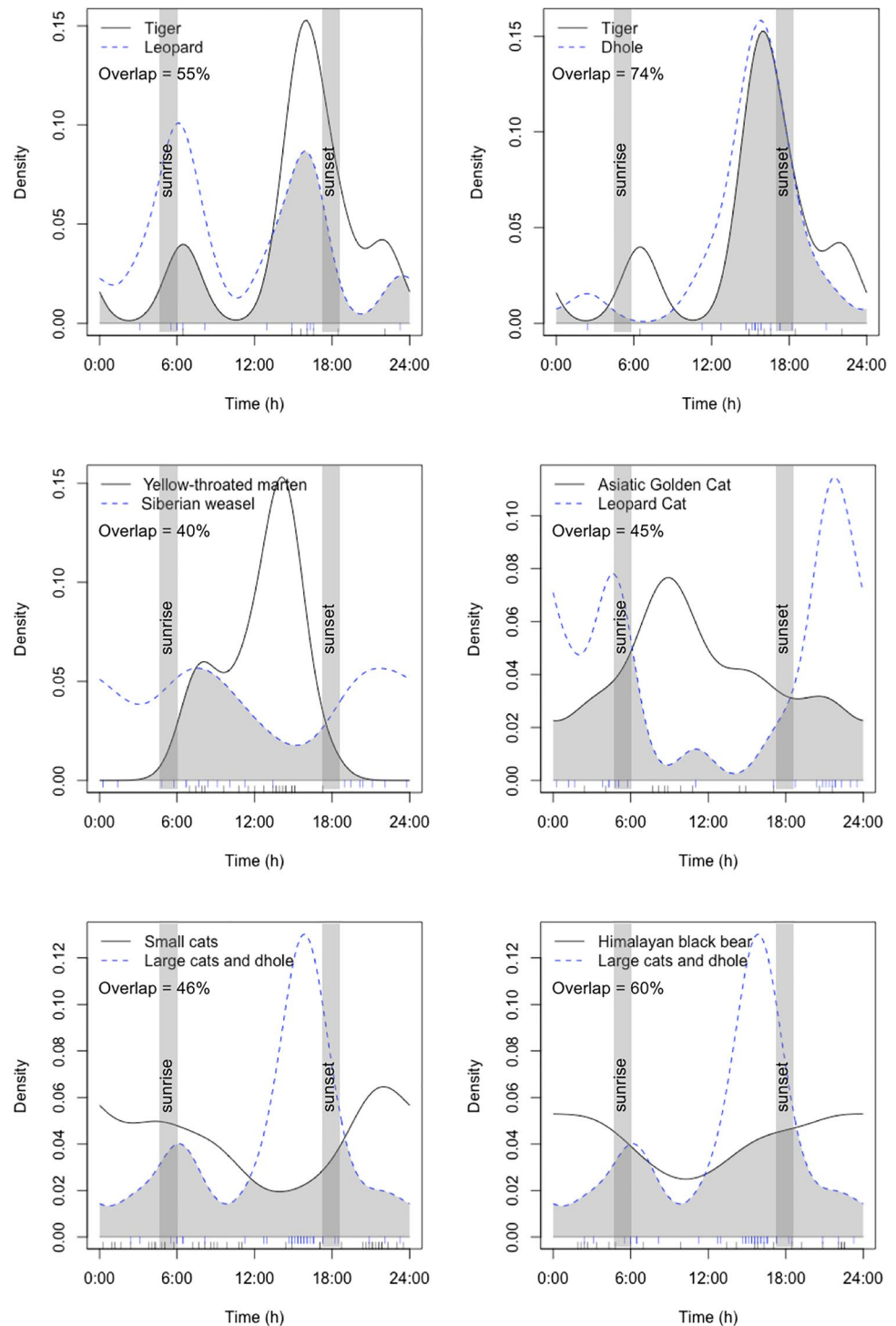
Of the 13 carnivore species detected in our study, four species are globally threatened on the IUCN Red List. These comprise the endangered tiger and dhole, and the vulnerable common leopard and Asiatic black bear. Although the Asiatic golden cat and marbled cat are listed as near threatened, their global populations are deemed to be declining. Global populations are also declining for three species of least concern detected in our study, which are the yellow-throated marten, Himalayan palm civet, and spotted linsang. Given the overall species richness combined with the presence of

both threatened and declining populations of near threatened species, the montane forest zone in Bhutan is important for regional carnivore conservation in the Eastern Himalayas.

Large carnivore patterns

Although large carnivores had overlapping distributions, they appeared to restrict spatial occurrence by rarely overlapping at camera sites. Tiger, leopard, and dhole are large, wide-ranging carnivores that occur throughout much of Bhutan (Sangay and Vernes 2008), and each species was detected at between six (tiger and leopard) and seven (dhole) camera sites. All three species never overlapped at any one camera site, while overlap between tiger and leopard, leopard and dhole, and tiger and dhole only occurred at one camera station, with non-random statistical support for comparisons. Significant non-random co-occurrences were also detected between the Asiatic black bear and most other large carnivores. Tiger and leopard co-occurrence was not significantly less than expected. However, because these species occupied different ends of the elevation gradient and typically occupied different forest types, they appeared to be largely segregated at the landscape scale in our study area and spatially avoided each other. At another study site in central Bhutan, Thinley et al. (2018) found evidence that large predators were sympatric at the landscape scale, but were spatially segregated at finer scales. In that study, tiger, leopard, and dhole were never captured on a camera trap at the same location, on the same day, or during the same 2-week sampling occasion despite each species occurring throughout the study area. The ecological dominance of tigers over leopards is well documented (Morse 1974; Steinmetz et al. 2013) and is probably responsible for the patterns we observed. For

Fig. 2 Temporal overlap between species and species groupings from camera trap data. **a** Tiger (*Panthera tigris*) and leopard (*Panthera pardus*), **b** tiger and dhole (*Cuon alpinus*), **c** yellow-throated marten (*Martes flavigula*) and Siberian weasel (*Mustela sibirica*), **d** Asiatic golden cat (*Catopuma temminckii*) and leopard cat (*Prionailurus bengalensis*), **e** small cat group (golden cat, leopard cat and marbled cat, *Pardofelis marmorata*) and large cats and dhole group (tiger, leopard and dhole), and **f** Himalayan black bear (*Ursus thibetanus*) and large cat and dhole group

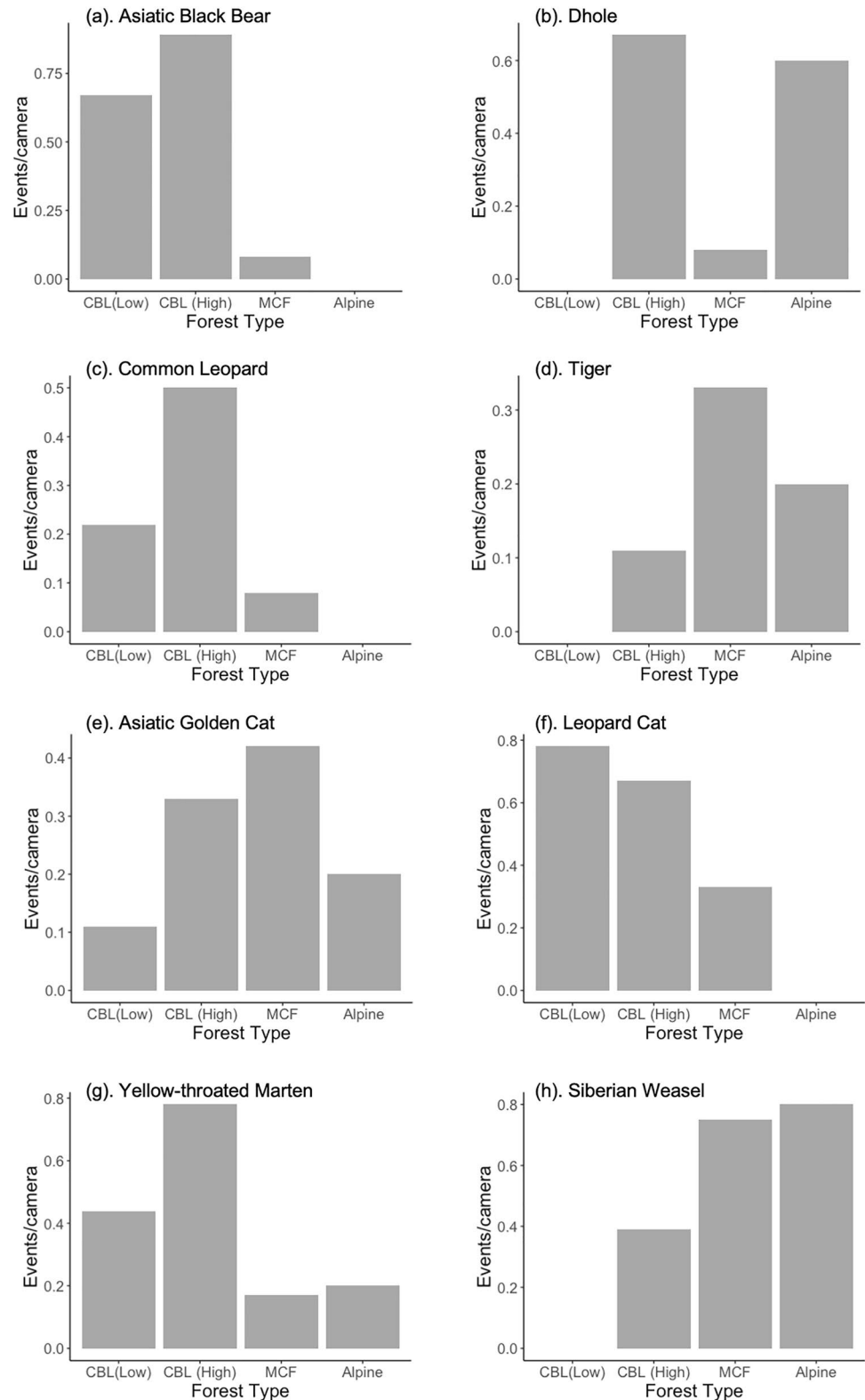


example, Seidensticker (1976) showed that leopards avoided areas frequented by tigers in Nepal's Chitwan National Park. Similarly, Odden et al. (2010) found significantly higher leopard signs near the periphery of a tiger's home range in Nepal's Bardia National Park rather than closer to the tiger's home range core area, while Steinmetz et al. (2013) showed that tiger occurrence in Thailand's Kuiburi National Park

was driven by prey availability with leopard and dhole distribution concurrently influenced by their avoidance of tigers. However, Allen et al. (2020) showed high temporal overlap between the dhole and tiger in Sumatra, and attributed it to lack of fear by pack-hunting dholes toward the tiger.

Prey availability can influence the degree of spatial and temporal separation in carnivore guilds. Karanth et al.

Fig. 3 Number of independent events per camera trap for cameras set in cool broadleaf forest (CBL) at low (2000–2700 m) elevation (“CBL(Low)”), cool broadleaf forest at mid (2700–3500 m) elevation (“CBL(High)”), mixed conifer forest at mid (2700–3500 m) elevation (“MCF”), and sub-alpine vegetation at high (> 3500 m) elevation (“Alpine”) for the eight most commonly detected mammals in the study area



(2017) demonstrated that local prey resource availability influenced the behavior of tigers, leopards, and dhole in Southern India. At low prey density, spatial overlap between all three species was high as each sought to maximize prey

acquisition against the trade-off of an antagonistic encounter. However, when prey density was high, the three species avoided encounters through fine-scale spatial segregation. We recorded several prey species on camera traps

but it was not possible to determine empirically whether prey density at our study site was higher or lower relative to other regions. Nevertheless, Bhutan's forests are largely intact landscapes supporting diverse mammal communities not overtly impacted by high livestock densities or human hunting pressure. Although livestock predation is present (Sangay and Vernes 2008), predation rates are considered tolerable (Sangay and Vernes 2014), perhaps indicating that Bhutan's large predators are subsisting largely on abundant native prey species. Furthermore, native ungulates (principally barking deer *Muntiacus muntjac*, sambar *Rusa unicorn*, and wild pig *Sus scrofa*) were detected three times more often on our camera traps than livestock, indicating relatively high native prey densities.

Small carnivore patterns

Small felids in our study also temporally avoided larger felids and the dhole. Pasanen-Mortensen et al. (2013) indicated a negative correlation between relative abundance of apex and mesocarnivores due to direct dominance by apex predators (Oliveira and Pereira 2014). Mesocarnivore species subsequently adopt spatiotemporal segregation to allow coexistence (Bitetti et al. 2010). Zhao et al. (2020) discovered a similar pattern in China whereby mesocarnivores (leopard cat, red fox, Asian badger *Meles leucurus*, Siberian weasel, Himalayan palm civet, and yellow-throated marten) spatially and seasonally avoided leopards. Similarly, Allen et al. (2020) found that leopard cats and Asian golden cats temporally avoid the tiger in Sumatra.

Smaller mesopredators in our study also displayed interspecific avoidance, possibly based on intra-guild aggression and/or resource competition. Three small felids (leopard cat, Asiatic golden cat, and marbled cat) common to Bhutan's mid-altitudinal forests were detected at our study site but interspecific overlap at a camera trap station was rare, with strong statistical support for this non-random pattern. The Asiatic golden cat, the largest of the small felids in the study area, had a diurnal activity schedule whereas the smaller leopard cat was strongly nocturnal. Leopard cats are typically nocturnal (Bu et al. 2016; Johnson et al. 2009) to maximize encounters with small rodents, which are their primary prey (Austin et al. 2007; Grassman et al. 2005; Rajaratnam et al. 2007). Similar temporal activity partitioning has also been detected for Asiatic golden cats and leopard cats in Northern Laos to help facilitate coexistence (Rasphone et al. 2020).

The yellow-throated marten and Siberian weasel were the most common mustelids in our study. However, both species exhibited strong spatial partitioning, occurring together at only 3 of the 27 camera trap sites utilized by this species pair. They also exhibited little temporal overlap. Yellow-throated martens were diurnal while Siberian weasels were

largely nocturnal. Yellow-throated martens are considered to be dominant over the smaller Siberian weasel, and there is evidence from other studies that spatial and temporal partitioning occurs. Bu et al. (2016) showed that the diurnal yellow-throated marten in China switched to feeding on small mammals in winter due to lack of fruit. Concurrently, Siberian weasels which until then had no clear diel activity pattern, switched to being nocturnal. Bu et al. (2016) argued that because Siberian weasels also prey predominantly on small mammals (Bu et al. 2016; Chiang et al. 2012), they switched activity to minimize interactions with the larger, dominant yellow-throated marten. Similarly, Chiang et al. (2012) found that Siberian weasels were mostly nocturnal in southern Taiwan where they co-occurred with yellow-throated martens, while Wong (1997) found weasels were more diurnal at a Taiwanese site where yellow-throated martens were absent. Contrastingly, Zhao et al. (2020) revealed at another site in China that Siberian weasels and yellow-throated martens were mainly diurnal, but spatially avoided each other and were temporally segregated from other mesopredators. Similar temporal shifts in activity have been recorded for other mesopredators. For example, Harrington (2007) showed invasive mink (*Mustela vison*) in the UK switched activity from predominantly nocturnal to predominantly diurnal in the presence of a larger aggressive competitor, the Eurasian otter (*Lutra lutra*).

Our study has shown that 13 different carnivores are able to co-occur within a relatively small area through non-random spatial and temporal partitioning to facilitate co-occurrence. Leopards and dhole appeared to avoid tiger, smaller cats and mustelids avoided one another, and the smaller Siberian weasel avoided the much larger yellow-throated marten. Our work was, however, undertaken over a relatively small timeframe in only one small area of the Himalaya. Nevertheless, this initial understanding of spatial and temporal segregation in a montane carnivore guild can inform future carnivore conservation especially through its applicability to alleviate potential human-wildlife conflict. Livestock in Bhutan are commonly grazed untended in a landscape shared by sympatric predators, resulting in opportunistic livestock depredation (Rajaratnam et al. 2016; Sangay and Vernes 2008) by the four IUCN-listed threatened large carnivore species (tiger, common leopard, dhole, and Asiatic black bear) detected in our study. Despite being deemed as tolerable (Sangay and Vernes 2014), livestock predation has socioeconomic repercussions on rural agropastoralists which can possibly lead to retaliation (Din et al. 2017). As such, knowledge of carnivore spatial and temporal activity can guide improved livestock husbandry by modifying grazing patterns and timing, including provisions for tethering in villages (Katel et al. 2015; Rajaratnam et al. 2016; Sangay and Vernes 2008). Our study lays the foundation to further investigate spatiotemporal patterns within

Himalayan carnivore guilds over seasonal time frames, and across a larger geographical area. This expanded research scope can help determine if carnivore species are modifying behavior or populations are under stress from anthropogenic impacts.

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