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Original investigation

Distribution and activity pattern of stone marten *Martes foina* in relation to prey and predators



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ABSTRACT

Small carnivores are expected to optimize their activity to maximize prey capture and minimize their encounter with predators. We assessed the activity pattern of the stone marten *Martes foina* in relation to its potential prey, the Himalayan woolly hare *Lepus oiostolus* and the Royle's pika *Ochotona roylei*, and its predators, the red fox *Vulpes vulpes* and the free-ranging dog *Canis familiaris*. Using three years of camera trapping data from the Indian Trans-Himalaya, we estimated individual and pair-wise spatio-temporal niche width and overlap, respectively, using Levins' asymmetric index. Stone martens showed limited space use (spatial niche width 0.16) and nocturnal activity (temporal niche width 0.35). They had high temporal (0.75) and low spatial overlap (0.05) with hares; while they had relatively low temporal (0.33) but higher spatial overlap (0.29) with pikas. Red foxes showed relatively high temporal (1.21) and spatial (0.75) overlap with martens, while free-ranging dogs showed low temporal (0.23) and spatial (0.03) overlap with martens. Although restricted space and time use by pikas might help martens track pikas even with relatively low spatio-temporal overlap, martens may be benefiting from higher temporal overlap with hares. While martens seem to be co-existing with foxes, their nocturnal activity might be driven by a trade-off between consuming prey and avoidance of diurnal predators like dogs.

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Introduction

Understanding temporal and spatial activity patterns can provide an insight into competition and resource partitioning mechanisms among sympatric species (Schoener, 1974). The activity pattern of a species is shaped by competition and predation (Kronfeld-Schor and Dayan, 2003). In small carnivores, major factors affecting their activity patterns are their access to prey, competition with other small carnivores, and predation by larger carnivores (Bischof et al., 2014). The small carnivore group is smaller in size and mass compared to other apex-predators and mesocarnivores (Mudappa, 2013). The small carnivore assemblage in India comprises of 32 species in the families Ailuridae, Herpestidae, Mustelidae, Prionodontidae, Viverridae and other species of small cats (Mudappa, 2013). Most small carnivores share their space with larger predators which increases chances of interference competition and also intra-guild predation. Thus, a "landscape of fear" is induced upon small carnivores by larger carnivores, forcing small carnivores to modify their activity patterns to reduce

* Corresponding author at: #361, "Hari hara", 5th main, 1st cross, Canara Bank Layout, Kodigehalli, Bangalore, 560097, Karnataka, India. *E-mail address:* suhridam@ncf-india.org (S. Roy). encounters with larger predators, but without affecting prey capture (Ritchie and Johnson, 2009). Most of the studies addressing spatio-temporal partitioning among mammalian carnivore assemblage have focused on large to medium-sized species, however, information on small carnivores, including members of Mustelidae, is limited (Mudappa, 2013; Bischof et al., 2014).

The Himalayas and its foothills are one of the strongholds of small carnivore diversity in India, and at high altitudes the mustelids tend to dominate the small carnivore community (Mudappa, 2013). Within mustelids, stone martens (*Martes foina*) are a small sized (1.1–2.3 kg; Menon, 2014) versatile carnivore with a wide distribution throughout much of Europe and Central to Southeast Asia up to northern Myanmar, occurring from sea level to the high-altitudes (Abramov et al., 2016). In India, stone martens occur along the Himalayas and marginal mountains of the Tibetan Plateau, and the Trans-Himalaya (Mudappa, 2013).

Stone martens are mostly nocturnal (Monterroso et al., 2014; Bischof et al., 2014; Torretta et al., 2017), but there have also been reports of diurnal activity (Posillico et al., 1995). They are a generalist feeder and their diet may vary with seasonal and regional food availability (Serafini and Lovari, 1993; Padial et al., 2002). During summer and autumn, martens' diet is mainly composed of plant matter followed by small mammals like rodents and lagomorphs, but during the winter and spring, consumption of animal

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matter increases significantly with a high proportion of small mammals and invertebrates (Serafini and Lovari, 1993; Padial et al., 2002). Martens are also known to shift from rodents to other small sized mammals, e.g. hares and rabbits, based on prey availability (Thompson and Colgan, 1990; Monterroso et al., 2013; Carvalho and Gomes, 2004).

We assessed the spatial and temporal activity pattern of stone martens in relation to four other species - two of its potential small-sized wild-prey, Himalayan woolly hares (Lepus oiostolus) (2.5–3 kg) and Royle's pikas (Ochotona roylei) (0.10–0.15 kg) (Menon, 2014); a larger sized carnivore, free-ranging dogs (Canis *familiaris*) (mean body-mass \sim 14.7 kg; Butler et al., 2004); and a potential native competitor and predator, red foxes (Vulpes vulpes) (3-14 kg; Nowak and Paradiso, 1983). This study was conducted in the Trans-Himalayan Spiti Valley, Himachal Pradesh, India. Stone martens, being smaller in size, are likely to face competition from red foxes (Padial et al., 2002; Papakosta et al., 2010), and there are reports of red foxes occasionally killing stone martens (Padial et al., 2002). There has been no documentation of free-ranging dogs interacting with stone martens. However, Eurasian badgers (*Meles meles*), a mustelid with a body weight (10–16 kg; Nowak and Paradiso, 1983) comparable to red foxes, has been reported to face spatial exclusion by dogs (Revilla et al., 2001). Chilla foxes, a mesocarnivore, has also been reported to face interference competition and occasional predation by dogs (Silva-Rodríguez et al., 2010). Stone martens, being relatively smaller in size compared to badgers and foxes, might face competitive exclusion and/or predation by free-ranging dogs. Free-ranging dogs are also known to transmit diseases, harass or kill wildlife, and compete with native and endemic species (Ghoshal et al., 2016; Young et al., 2011).

We expected the activity pattern and space use of stone martens to be similar to their prey, and to differ from red foxes and freeranging dogs. We used three years of camera trap data to assess and compare diel activity patterns.

Material and methods

Study area

The study was carried out across an area of ca. 2000 km² in the Spiti sub-division of Lahaul and Spiti district (32° 37' N, 77° 25′ E), Himachal Pradesh, northern India, across three years (Fig. 1). The Spiti valley is formed by the Spiti River, originating from Kunzum la (la - pass) and draining into the Sutlej in neighboring Kinnaur. The landscape on the left bank of the Spiti River is dominated by a high-elevation (>4200 m) rolling plateau, while the right bank is relatively more rugged and steep (USL, 2011). The Trans-Himalaya is a cold-desert ecosystem, characterized by a short growing season (May-August) and extreme winter (November-March) (Suryawanshi et al., 2010). The vegetation is categorized as 'dry alpine steppe' (Champion and Seth, 1968). Human population density is low in the study area (2 individuals/km²) (Ministry of Home Affairs Report, 2011). The primary livelihood of the local people is agro-pastoralism. The livestock assemblage in Spiti includes yak, cattle, cattle-yak hybrids (males and females called dzo and dzomo, respectively), horse, donkey, sheep, and goat. Livestock is grazed in the pastures through spring, summer, and autumn (Mishra et al., 2004).

In this landscape, two small sized mammals of the order Lagomorpha, woolly hares and Royle's pikas, and murid rodents can be potential mammalian prey for stone martens and red foxes. In the Indian Trans-Himalaya, free-ranging dogs mainly scavenge on anthropogenic garbage (Ghoshal et al., 2016), but they are also a major predator of livestock (Suryawanshi et al., 2013; Home et al., 2017).

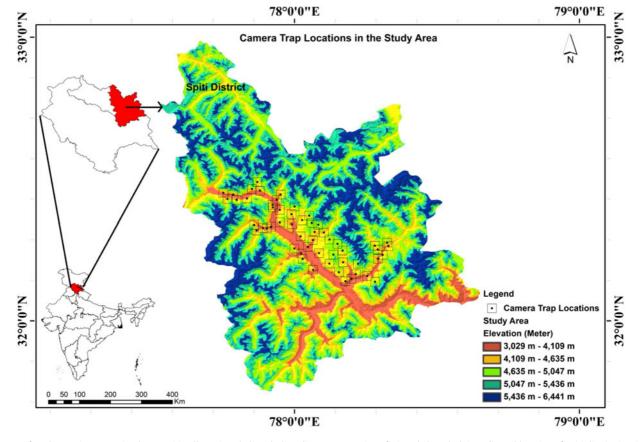


Fig. 1. Map of study area in Trans-Himalayan Spiti valley, Himachal Pradesh, India. Inset: Location of Himachal Pradesh in India and location of Spiti district in Himachal Pradesh.

Study design and method

We deployed camera traps at 57 locations (Fig. 1) using either Reconyx RapidFireTM RM45 or Reconyx HyperFireTM HC500 or Reconyx RapidFireTM RC55, from November 2013 to October 2015, with an effective trap effort of 8843 days. Camera traps were placed in a 3 km x 3 km grid following the trap design used by Sharma et al. (2015). In 2013, a total of 38 camera traps were deployed at 38 locations on the left bank of Spiti River (November - December). In 2014, on the left bank of Spiti river, 13 locations were discontinued for camera trap monitoring, while one new location on the left bank and 14 new locations on the right bank were added. Camera traps were deployed on the left and right banks of Spiti River from January to May 2014 and July to October 2014, respectively. In 2015, on the left bank, camera traps were deployed at eight new locations from May to October and monitoring was discontinued for eight other locations. Overall 57 sites were covered across 13 effective camera-trapping months. The main study targeted the population estimation of snow leopards, and the camera traps were placed on the basis of snow leopard signs. The home range size of stone martens varies from 0.12 to 2.11 km² (Nowak, 1999). The home range size of red foxes ranges from 0.45 to 9.28 km² (Trewhella et al., 1988). To ensure camera traps were spatially independent, we used a 3 km x 3 km grid design which is expected to be in accordance with the small home ranges of the study species. Camera traps were programmed to take five images from the time the subject comes within the range of camera sensor to the time the subject leaves the range. The photographic captures provided data on space and time use of stone martens and other study species. We excluded snow leopards from the analysis as the effect of snow leopards on stone martens was expected to be lesser than that of red foxes and free-ranging dogs due to the difference in body size (Donadio and Buskirk, 2006). Photographic captures of wolves and rodents were too low, so we dropped them from the analyses.

Analyses

Each year's data was imported into LibreOffice database using R (R Core Team, 2016). Each photograph was categorized by its species, activity, and the number of individuals of a species captured in the photograph. Each photograph was given a unique occasion number with a gap of at least 15 min between consecutive occasions. The occasion number refers to one unique capture event

of an individual or a group of a single species, on a camera trap. Multiple photographs within 15-minute intervals were considered a single event.

All the unique capture events for 24 h were obtained for each of the study species across the study duration. For each hour and each species, the proportional time-use (capture events of a species for that hour / total capture events of that species across 24 h) was calculated, and this matrix was used to assess temporal overlap using Levins' overlap index (Levins, 1968): $O_{ik} = \sum p_{ij}p_{ik} / \sum p_{ij}^2$, where O_{ik} is the niche overlap of species k with species j, and p_{ij} and pik represent the proportions that a resource state i contributes to the resource use of species j and k. Levins' index (Levins, 1968) is asymmetric, where the overlap of the first species with the second can differ from the second with the first. It separately estimates the extent to which the first species overlaps with the second and vice versa. Levin's index (Levins, 1968) can range from 0 (no overlap) to 1 (or slightly higher than 1; complete overlap). The species with high niche width might form extensive overlap with a species with low niche width and such extensive overlap can sometimes marginally cross the upper limit of 1. We calculated space use for each species for each location using an event capture rate per 100 trap days (capture events for the location / trap effort in that location X 100). We assumed event capture rates as the unit of space use of the species and used event capture rates for each location and across all locations to obtain proportional space use (space use of the species at one site / space use of the species across all sites) matrix for each species. Niche width of a species refers to the extent to which the niche category is being used by the species. To determine niche width of each species, we used Levins' index of niche width (Levins 1968) and standardized the results using Hurlbert's correction (Hurlbert, 1978). Niche width value can range from 0 to 1 (0 - no use; 1 - complete use of the niche category by the species). All temporal and spatial niche overlap and niche width analyses were performed using statistical software R (R Core Team, 2016) and package spaa: Species Association Analysis, R package version 0.2.1 (Zhang, 2013).

Results

A total of 5470 images of study species were captured across the sampling period between 2013 and 2015, from 8843 trap-days. Less than 1% of captured images were unidentifiable. Considering unique capture events, a total of 768 events of the five study

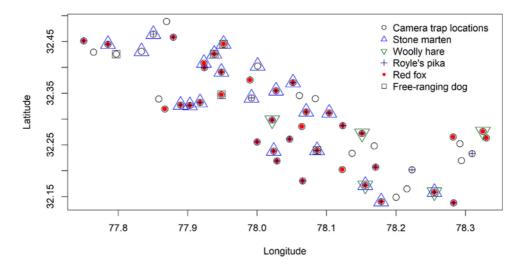


Fig. 2. Distribution and occurrence of study species across camera trap locations. Red foxes were captured at 38 sites, followed by Royle's pikas (31), stone martens (21), woolly hares (5) and free-ranging dogs (5) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

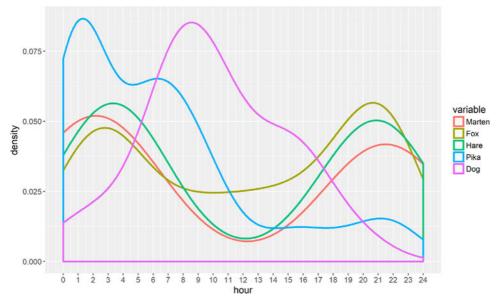


Fig. 3. Kernel density distribution graphs of capture events of different study species across 24 h.

species were recorded. Some events overlapped between consecutive hours, therefore grouping observations into hourly bins reduced total events to 764 on the temporal scale. We used 768 and 764 events for the spatial scale and for the temporal scale analyses, respectively.

Temporal and spatial activity patterns

Stone marten

Stone martens were captured at 53 unique events comprising 6.90% of the total events (Appendix A). They were captured at 21 out of 57 camera trap locations (Fig. 2). Stone martens showed a nocturnal (85%) activity pattern, with two activity peaks, between 2100 h–2300 h and 0100 h–0300 h (Fig. 3). The temporal and spatial niche widths were 0.35 and 0.16, respectively (Appendix C).

Red fox

Red foxes were captured at 391 unique events comprising 51.18% of total events (Appendix A). They were captured at 38 out of 57 camera trap locations (Fig. 2). Red foxes were primarily active during the night (1900 h – 0400 h) with two peaks of activity, between 2000 h - 2300 h and 0200 h - 0400 h (Fig. 3). The majority (54.15%) of the capture events of red foxes were during the night, but crepuscular (23.52%) and diurnal activity (25.32%) was also recorded (Fig. 3). Temporal and spatial niche widths were 0.79 and 0.34, respectively (Appendix C).

Free-ranging dog

Free-ranging dogs were captured at 28 unique events comprising 3.66% of the total events (Appendix A). Free-ranging dogs were captured at only 5 locations out of 57 (Fig. 2). Their activity pattern was mostly diurnal (71.42%) with limited nocturnal and crepuscular activity (14.28%) (Fig. 3). Their peak activity was around 0800 h – 1000 h (Fig. 3). Temporal and spatial niche widths were 0.49 and 0.02, respectively (Appendix C).

Royle's pika

Royle's pikas were captured at 180 unique events comprising 23.56% of the total events (Appendix A). They occurred at 31 sites out of 57 camera trap locations (Fig. 2). Their activity peak was observed between 0100 h and 0300 h, after which activity dropped gradually, but they were recorded throughout 24 h (diurnal: 48.33%, nocturnal: 29.44%, crepuscular: 22.22%) (Fig. 3). Temporal and spatial niche widths were 0.26 and 0.14, respectively (Appendix C).

Woolly hare

Woolly hares were captured at 112 unique events comprising 14.66% of total events (Appendix A). They occurred at only 5 locations (Fig. 2). Woolly hares were primarily nocturnal (61.60%), with two peaks between 2000 h - 2300 h and 0100 h - 0400 h (Fig. 3). Crepuscular activity was also observed (35.70%). Temporal and spatial niche widths were 0.53 and 0.03, respectively (Appendix C).

Comparison of activity pattern across study species

Appendices D and E provide pairwise temporal and spatial overlap in Levins' index (1968), respectively. Stone martens and woolly hares had high temporal overlap (hare with marten: 1.07, marten with hare: 0.74) and low spatial overlap (hare with marten: 0.02, marten with hare: 0.05). Stone martens and pikas had medium temporal overlap (pika with marten: 0.26, marten with pika: 0.33) and medium spatial overlap (pika with marten: 0.27, marten with pika: 0.29). Red foxes had extensive temporal overlap with stone martens (fox with marten: 1.21, marten with fox: 0.58). Red foxes had higher spatial overlap with stone martens than vice versa (fox with marten: 0.75, marten with fox: 0.36). Free-ranging dogs had low spatial and temporal overlap with all other study species including martens. The only exception was the temporal overlap of dogs with pikas (0.47).

Overlap of red foxes with hares (temporal: 1.08, spatial: 0.98) was much higher than of hares with foxes (temporal: 0.74, spatial: 0.13). The overlap of red foxes with pikas (temporal: 0.71, spatial: 0.57) was much higher than of pikas with foxes (temporal: 0.26, spatial: 0.26).

Discussion

Stone martens were nocturnal, in line with our expectation and previous findings (Monterroso et al., 2014; Bischof et al., 2014; Torretta et al., 2017). The temporal activity pattern of stone martens closely followed that of woolly hares, resulting in high temporal overlap between hares and martens, which might facilitate higher predation success for martens (Fig. 4). Woolly hares had very low

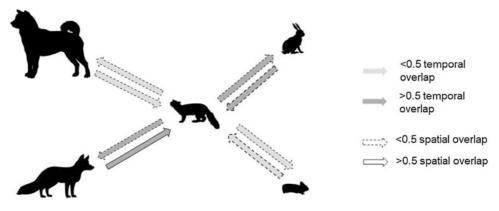


Fig. 4. Patterns of interaction of stone martens with other study species.

spatial niche width, indicating limited space use. Hunting at a time of day when the probability of prey capture is highest, may allow greater prey capture success at a lower energetic cost (Zielinski, 2000). Thus, stone martens can increase their chances of capturing spatially concentrated prey like hares by increasing temporal overlap. However, the low overlap in spatial niche axis might facilitate hares to escape predation. Although stone martens occurred widely in our study area (21 of the 57 cameras), their narrow niche width suggests that they are probably specific in their use of habitats. Pikas were widespread (31 out of 57 locations), and were active for all 24 h, but showed narrow temporal and spatial niche width, which suggests a relatively high use of particular sites during certain time periods. Thus, even with medium temporal and spatial overlap with pikas, stone martens might track the species because of its concentrated space and time use (Fig. 4). Pikas are an important prey species for stone martens (Flux and Angermann, 1990), and in high altitudes of the Pamir and the Karakoram Mountains, Bischof et al. (2014) found that stone martens were more likely to use those sites where pikas were present.

We expected that the nocturnal activity pattern of stone martens was for better cover from larger predators and potential competitors, such as free-ranging dogs and red foxes. Red foxes had a higher temporal and spatial overlap with stone martens than vice-versa, indicating a higher impact of foxes on martens, a smaller carnivore (Fig. 4). High habitat overlap (Pereira et al., 2012) and dietary overlap (Serafini and Lovari, 1993; Papakosta et al., 2010; Petrov et al., 2016) between stone martens and red foxes have been reported previously, suggesting that stone martens, as a smaller predator, might face competition from red foxes. Bischof et al. (2014) found a higher probability of stone martens avoiding sites used by red foxes. Previous studies have reported competition between stone martens and red foxes, and even intra-guild killing of martens by foxes (Padial et al., 2002). Dietary overlap is known to increase between red foxes and stone martens during winter and spring (Serafini and Lovari, 1993; Padial et al., 2002). Since availability of food varies significantly across seasons in the Indian Trans-Himalaya, high niche overlap in space and time might imply potential for competition between foxes and martens, especially during winter. However, previous studies suggest that there might be several mechanisms of coexistence between stone martens and red foxes, e.g. segregation of niche axes at macro levels like selection of different habitats (Duduś et al., 2014; Petrov et al., 2016), and at micro levels like shifting of peak activity at different moon phases (Petrov et al., 2016) or diel phases (Torretta et al., 2017). Competition can also be reduced by sequential use of different prey species which have different peak activity periods (Monterroso et al., 2014; Torretta et al., 2017).

Stone martens and free-ranging dogs showed low temporal and spatial overlap, in line with our expectation. Free-ranging dogs

were mainly active during the daytime, and their density is closely associated with the village size and garbage availability in the region (Ghoshal et al., 2016). This suggests that stone martens might reduce their interaction with free ranging dogs through their nocturnal activity pattern and selective habitat and space use (Fig. 4).

Conclusion

We analyzed the activity patterns of stone martens in the Indian Trans-Himalaya in relation to their potential prey species, Himalayan woolly hares and Royle's pikas, and two larger predators, red foxes and free-ranging dogs. Our data suggested that stone martens' temporal activity pattern was nocturnal and closely followed that of woolly hares'. This could allow stone martens to increase their chances of capturing hares, and at the same time avoid larger diurnal predators like dogs. Royle's pikas could provide an additional source of food to stone martens because of their restricted space and time use.

Our results showed a potential for competition between stone martens and red foxes, given the high temporal and spatial overlap between these species. However, the mechanisms of coexistence of these mesocarnivores in the context of other broad niche categories and fine scale categories (e.g. lunar cycle) in the Trans-Himalayan landscape needs to be further investigated.

Author contribution

KRS & SR conceived and developed the idea. AB led the field work. KRS built the database system. SR, KRS and AG conducted the analyses. SR wrote the manuscript. KRS and AG reviewed the manuscript.

Declarations of interest

None.

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Appendix A. Number of events captured each hour for each study species, across 24 h

Hour	Stone marten	Red fox	Woolly hare	Royle's pika	Free ranging dog
0 - 1	8	25	7	6	1
1 – 2	2	14	4	59	0
2 – 3	6	25	8	4	1
3 – 4	7	26	12	4	1
4 - 5	5	19	11	5	0
5 – 6	1	20	9	14	0
6 – 7	0	5	5	16	2
7 – 8	1	7	1	13	3
8 - 9	0	10	1	10	4
9 - 10	0	13	1	12	2
10 – 11	0	6	0	5	3
11 – 12	0	9	0	4	2
12 – 13	0	12	1	1	1
13 – 14	0	9	0	0	0
14 - 15	0	10	0	2	2
15 – 16	0	10	0	4	2
16 – 17	0	13	0	2	1
17 – 18	0	9	3	2	2
18 – 19	0	12	7	2	0
19 – 20	1	27	4	1	0
20 – 21	4	24	7	3	1
21 – 22	7	26	10	3	0
22 – 23	5	34	9	5	0
23 - 24	6	26	12	3	0

Appendix B. Events captured across different camera trap locations for different study species

Location	Camera trap id	Stone marten	Red fox	Free ranging dog	Royle's pika	Woolly hare	Total trap days
Bandang	1	6	11	0	6	0	304
Before Sharma Nalla	2	0	0	0	2	0	44
Chicham River side	3	0	1	1	0	0	262
Chuprang Top	4	0	0	0	0	0	184
Chuiling	5	0	4	0	2	4	183
Chuldim nalla	6	1	2	0	2	0	178
Dozom_Phu	7	0	0	0	0	0	27
Hansa Tokpo	8	1	0	0	2	0	315
Kibri nalla	9	0	5	0	4	0	164
Kakti nalla1	10	0	2	0	0	0	102
Kholaktsa	11	4	30	0	89	0	315
Kindasa	12	0	23	0	3	0	316
Ladarcha	13	4	8	0	3	0	322
Laksha pang	14	0	5	0	0	1	44
Lukdur nalla	15	0	0	0	0	0	306
Makhang Phu	16	0	4	0	0	0	138
Nema Kukur	17	0	4	0	1	0	339
Pangsham Top	18	0	0	0	0	0	172
Phalangri top	19	4	9	0	1	0	184
Phelah1	20	0	42	0	2	0	179
Phipuk top	21	0	4	0	0	0	23
Phunam_dongo	22	0	21	0	6	48	186
Rangrik pee	23	0	13	0	2	0	172
Rijing	24	0	2	0	0	0	170
Sharma_Nalla_1	25	0	0	0	0	0	39
Sharma_Nalla_2	26	0	0	0	0	0	19
Sharma_Nalla_3	27	0	2	0	0	0	36
Takli	28	1	7	2	0	0	178
Takli_Nalla	29	2	15	20	8	0	314
Takphuk	30	1	15	4	2	0	323
Talache Ridgeline	31	0	0	0	0	0	35
Thaknak	32	0	9	0	0	0	181
Thaltak	33	1	0	0	0	0	173
Thuna_Nalla	34	0	0	0	0	0	288
Thuna_Nalla_Right_Side	35	0	1	0	1	0	50
Tishuu	36	0	0	0	0	0	170
Tsankar	37	1	1	0	1	0	147
Tseerigyuth	38	3	27	0	3	0	186
Youlsapang1	39	1	55	0	5	56	335
phela2	40	0	0	0	0	0	154
Kakti	40	0	0	0	2	0	32
Zango Kibri	41 42	1	1	0	4	3	96
	42 43	3	0	0		3	
chicham nalla	43	د	U	U	2	U	146

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Rahtangh inside	44	4	2	0	2	0	91
Chichong Top	45	0	0	0	0	0	98
Gha Tokpo (Kiamo)	46	0	0	1	0	0	96
Kiamo Dupuk	47	1	0	0	0	0	96
Phaldar Top	48	1	1	0	0	0	96
Nyu Lungba	49	0	12	0	3	0	96
Gyundi Top	50	0	0	0	0	0	96
Batal	51	0	2	0	0	0	96
Gyundi Nalla Side	52	2	10	0	4	0	96
Gyundi Channel	53	8	19	0	1	0	96
Hull Top	54	3	16	0	7	0	96
Rangrik IPH Sight	55	0	2	0	2	0	84
Kawang top	56	0	1	0	9	0	92
Queling top	57	0	5	0	1	0	83
Total		53	393	28	182	112	8843

Appendix C. Levins' (1968) temporal and spatial niche width (standardized) of study species

Species name	Temporal niche width	Spatial niche width	
Stone marten	0.35	0.16	
Red fox	0.79	0.34	
Free-ranging dog	0.49	0.02	
Woolly hare	0.53	0.03	
Royle's pika	0.26	0.14	

Appendix D. Levins' (1968) temporal overlap among study species. Species written in columns had overlap with species written in rows. Overlap values >0.50 are shown in bold

	Stone marten	Red fox	Free-ranging dog	Woolly hare	Royle's pika
Stone marten		1.21	0.23	1.07	0.26
Red fox	0.58		0.35	0.74	0.26
Free-ranging dog	0.17	0.55		0.25	0.27
Woolly hare	0.74	1.08	0.23		0.29
Royle's pika	0.33	0.71	0.47	0.53	

Appendix E. Levins' (1968) spatial overlap among study species. Species written in columns had overlap with species written in rows. Overlap values >0.50 are shown in bold

	Stone marten	Red fox	Free-ranging dog	Woolly hare	Royle's pika
Stone marten		0.75	0.03	0.02	0.27
Red fox	0.36		0.04	0.13	0.26
Free-ranging dog	0.14	0.33		0	0.15
Woolly hare	0.05	0.98	0		0.22
Royle's pika	0.29	0.57	0.04	0.06	

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