BJNRD (2025), 12(2): 5-18
Bhutan Journal of Natural Resources & Development

Research Article

www.bjnrd.org

Open Access

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

DOI: https://doi.org/10.17102/cnr.2025.108

Prey Occupancy and Functional Connectivity in Biological Corridor Seven, Bhutan

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Abstract

Biological corridors with a healthy prey base support predator dispersal, yet studies that combine occupancy and connectivity remain limited. This study evaluated six ungulate prey species in Biological Corridor Seven, Bhutan. Thirty-one paired camera traps were deployed on a 3 km × 3 km grid in the first half of 2025, yielding 5,144 trap days and 822 independent events. A hierarchical Bayesian multi-species occupancy model was fitted in PyMC (v5) to estimate occupancy (ψ) and detection probability (p) across winter, spring and summer. Predicted occupancy was mapped onto a 500 m × 500 m grid (N = 1,689 cells) and analysed with random-walk connectivity to identify movement routes and pinch points. Generalists showed high and widespread occupancy ($\psi = 0.933–0.981$), with peak detectability in winter ($p = 0.185–0.320$). In contrast, specialists were concentrated in narrow upper-elevation areas ($\psi = 0.639–0.877$), peaking in spring ($p = 0.085–0.164$). Connectivity analysis isolated seven macro pinch points and numerous conflict segments (< 500 m long) where linear infrastructure is likely to restrict movement. Priority mitigation include vegetated overpasses on dry slopes and bridge-style underpasses or culverts at riparian conflicts. A tiger *Panthera tigris* was recorded at two locations, indicating the use of the corridor by large predators. However, further studies on predator occupancy employing telemetry or genetics are recommended. Nonetheless, this integrated occupancy–connectivity framework may serve as a reproducible basis for prioritising mitigation and guiding adaptive corridor management under growing infrastructure development and climate pressure.

Keywords: Bayesian model, biological corridor, climate, connectivity, occupancy, pinch point, prey, tiger

Introduction

Ecological connectivity refers to the capacity of landscapes to facilitate the movement of organisms and ecological processes (Hilty et al., 2020). Corridors help maintain or restore that connectivity in otherwise fragmented landscapes (Rautela et al., 2022). When planned and managed appropriately, corridors support dispersal, gene flow, and climate-driven range shifts across elevational and latitudinal gradients (Deka et al., 2023; Soanes et al., 2024). International guidance recommends evaluating corridor effectiveness using both habitat condition (structural connectivity) and verified animal use, which indicates functional connectivity (Dickson et al., 2019; Hilty et al., 2020).

Connectivity science has advanced from single-species analysis toward community-oriented assessment. Studies from Himalayan systems show that the occurrence and move-

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Received: October 4, 2025
Accepted: November 16, 2025

Editor: Ugyen Dorji

ment of different mammals often concentrate in distinct habitat bands, implying that a design tailored to one focal species may overlook other pathways important for connectivity (Adhikari et al., 2024). Practice also shows there is no universal corridor width. Recommended widths depend on species, management goals and landscape setting (Adhikari et al., 2024; Ahmad & Gopi, 2024). Multi-species frameworks should explicitly include apex predators such as the tiger *Panthera tigris*. Given that tigers' use of corridors is determined by prey availability and spatial distribution, prey occupancy can serve as an indicator of corridor use (Deka et al., 2023; Rautela et al., 2022). Pairing this multi-species framework with connectivity modelling can locate areas of preferential use and diagnose bottlenecks for targeted measures (Dickson et al., 2019; Downey, 2021).

Bhutan has established a protected-area network linked by biological corridors (Wildlife Conservation Division [WCD], 2010), yet peer-reviewed evidence for functional connectivity remains limited. Many assessments in Bhutan examine a single species in a single season, leaving uncertainty about the extent of animal movement and limiting inference for corridor management (Dorji et al., 2019; Letro et al., 2021). Despite legal designation of corridors, most work relies on structural proxies rather than verified animal use, and there is little integration of multi-species, multi-season occupancy modelling with a connectivity framework in a Bhutanese corridor context (Dorji et al., 2019; Letro et al., 2021; Penjor, 2022; WCD, 2010). This study addresses the gap by integrating community occupancy (multi-species, multi-season) with connectivity modelling to map movement concentration and identify priority segments for mitigation in Biological Corridor Seven (BC7).

BC7 links Wangchuck Centennial National Park (WCNP), Phrumsengla National Park (PNP) and Bumdeling Wildlife Sanctuary (BWS) (Divisional Forest Office of Mongar [DFOM], 2023). The corridor faces increasing pressure from transport, energy development and land-surface warming, elevating the value of verified functional linkages (DFOM, 2023; Druk Green Power Corporation Limited [DGPCL], 2025). Community occupancy is integrated with connectivity modelling so that occurrence, detectability and movement concentration are analysed within one coherent workflow (Amir et al., 2022; Devarajan et al., 2020; van Etten, 2017). The approach operationalises functional connectivity for management by projecting prey occupancy across the corridor, translating those patterns into movement flow, and isolating pinch points (narrow places where animals tend to pass through) where linear infrastructure and rivers may constrain passage. This framework may serve as a transparent and reproducible basis for decisions that balance development and biodiversity in a montane context.

The study estimated multi-species, multi-season occupancy (ψ) and detection probabilities (p) for six ungulate prey species, and mapped movement pinch points and prospective wildlife-crossing locations along roads and rivers in BC7.

Materials and Methods

Study Area

BC7 (27.40 to 27.83° N, 90.98 to 91.31° E; area: 419 km^2) forms the east-central corridor of Bhutan and links WCNP, PNP, and BWS (Figure 1). The corridor spans six gewogs/ blocks in Lhuentse district (Gangzur, Khoma, Menbi, Metsho, Minjay and Tsenkhar) and two in Mongar district (Tsakaling and Tsamang; DFOM, 2023). Elevation ranged from 797 m a.s.l. (metres above sea level) to 4,370 m, with broadleaf (74%) forming the dominant forest type, and others include chirpine, mixed conifer and fir forests in small pockets (Rai, 2022). The corridor encompasses a 15.6 km segment of the Kurichhu River, along with approximately 44 km of streams and 1,296 km of smaller tributaries, providing important riparian habitats (DFOM, 2023). Within BC7, the mean daily maximum temperature is 25.4 °C, and the mean daily minimum temperature is 10.3 °C, and district-wide precipitation for Lhuentse is 34 mm (National Centre for Hydrology and Meteorology [NCHM], 2025). Approximately 920 households depend on BC7's resources (DFOM, 2023). Planned linear infrastructure expansions, including the Dorjilung Hydropower Project (DHPP) dam, feeder roads and transmission lines, threaten to sever wildlife movements, underscoring the need to identify movement pinch points and inform mitigation in BC7 (DGPCL, 2025).

Sampling Design

Thirty-one stratified camera-trap stations were deployed between January and July 2025, on a 3 km × 3 km grid (Figure 1B), aligned with the home ranges of prey species as described by Wangchuk (2004). Block 1 contained 17 camera stations, Block 2 contained 14, and Block 3 contained 7, with the number of stations proportional to the area of each block. Each station hosted two camera traps (Panthera, Reconyx or Cuddeback models) mounted 30–40 cm above ground and spaced 3–8 m apart to avoid cross-triggering (Dorji et al., 2019). Stations were at least 1 km apart, reducing spatial autocorrelation (Letro et al., 2021; Penjor, 2022). Seasons were defined as winter (January–February), spring (March–May) and summer (June–July). Independence of detections was defined as images of the same species at the same station separated by ≥ 20 minutes, following Dorji et al. (2019) to reduce temporal autocorrelation. Independent events (*IE*) within each 7-day occasion were converted to binary detections (1/0) to build the site × occasion histories for the multi-species occupancy model (MSOM).

Species and Covariance Selection

Six ungulate species central to the predator-prey system of the eastern Himalaya were analysed (Letro et al., 2021; Penjor, 2022; Wangchuk, 2004). Prey species were classified as generalists (barking deer *Muntiacus muntjak*, sambar deer *Rusa unicolor* and wild pig *Sus scrofa*) and specialists (Himalayan goral *Naemorhedus goral*, Himalayan serow *Capri-*

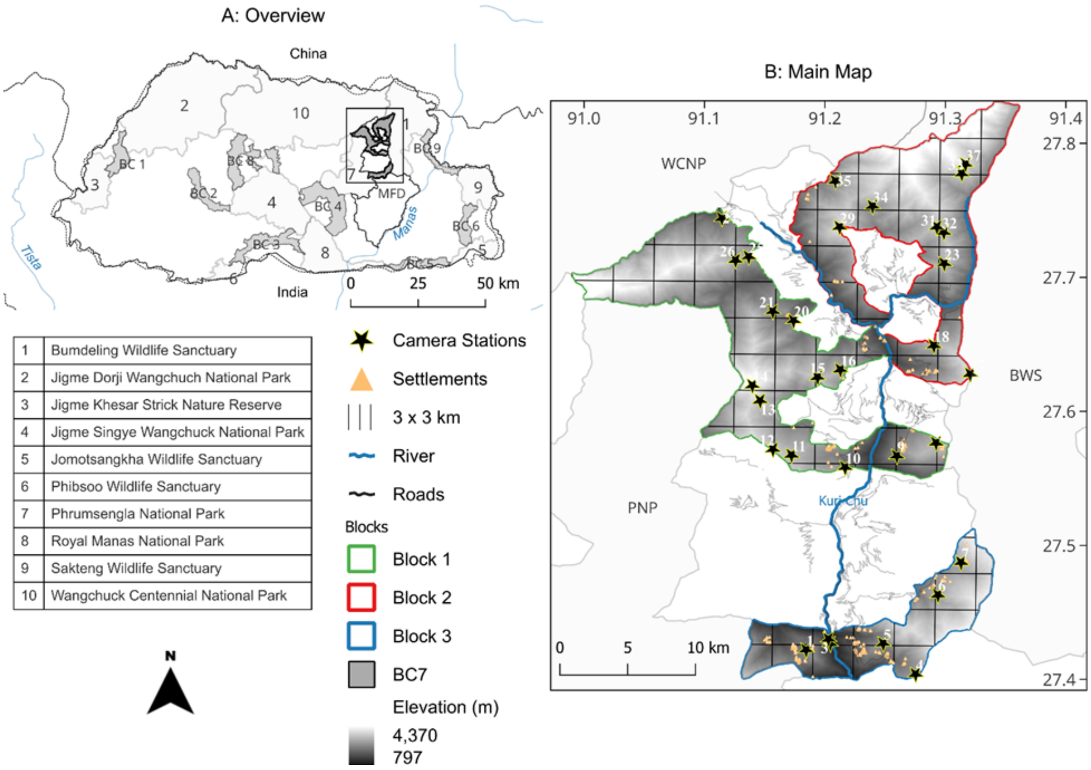

Figure 1: Study area and sampling design

cornis sumatraensis and musk deer *Moschus chrysogaster*) based on their elevational pattern and distribution following Wangchuk (2004). Detection histories were arranged in a 31 × 6 × 3 × 14 array (sites × species × seasons × seven-day occasions) following Devarajan et al. (2020).

Eight covariates (seven numeric, one categorical) were prepared in QGIS 3.40 (Qgis.org, 2024; Table 1). “Sample Raster Values” was used to extract canopy cover (Hansen et al., 2013), Human Footprint Index [HFI] (Venter et al., 2016), slope (from FABDEM; Hawker et al., 2022), precipitation and temperature (NCHM, 2025). “Join Attributes by Nearest” was used to compute distance to protected area (Department of Forests and Park Services [DoFPS], 2024) and to the nearest road (OpenStreetMap contributor, 2025). “Join Attributes by Location” assigned classes from land use and land cover (LULC2016; Rai et al., 2021) and forest types (Rai, 2022) to each station, combined as a single “LULC covariate.” Blue Pine Forest served as the

Table 1: Site-level covariates for 31 camera stations in BC7. CS – Camera Station (e.g., CS01), Can – canopy, Ds_PA – distance to protected areas, Ds_rd – distance to roads, Ds_set – distance to settlements, HFI – Human Footprint Index, Ppt – precipitation, Sl – slope, Tem – annual mean temperature, LULC – landuse – landcover, BPF – Blue Pine Forest, CBF – Cool Broadleaved Forest, CPF – Chirpine Forest, EOF – Evergreen Oak Forest, FIR – Fir Forest, HLF – Hemlock Forest, MCF – Mixed Conifer Forest, MDW – Meadows, WTR – Waterhole

CS	Can%	Ds_PA (m)	Ds_rd (m)	Ds_set (m)	HFI	Ppt (mm)	Sl%	Tem (°C)	LULC
1	86	1357	3213	217	0.003	75	17	15	CBF
2	58	3030	1616	957	0.015	70	28	21	CPF
3	0	3147	1387	701	0.003	70	50	20	CPF
4	87	5470	3333	981	0.061	129	2	14	EOF
5	87	6397	1574	801	0.021	129	16	14	EOF
6	94	3109	2018	370	0.025	121	15	12	EOF
7	0	1775	1751	350	0.004	115	22	11	MCF
8	89	858	2242	409	0.003	121	5	12	HLF
9	0	3489	2113	283	0.003	88	34	15	EOF
10	0	7160	1222	727	0.002	92	19	15	EOF
11	85	6226	3403	1643	0.002	116	6	11	EOF
12	0	4896	2864	823	0.019	110	9	11	MDW
13	0	1730	3180	2677	0.002	90	24	10	MCF
14	85	665	4707	3780	0.003	91	4	7	FIR
15	82	5402	2211	1883	0.003	111	23	10	BPF
16	54	7139	1419	721	0.003	116	16	12	CBF
17	12	68	2916	1913	0.002	105	2	9	FIR
18	0	1802	1550	1338	0.002	114	16	13	MDW
20	0	4602	3419	540	0.008	115	10	15	CBF
21	85	3411	2765	1101	0.003	115	16	14	EOF
23	85	2146	2822	1629	0.002	110	14	12	HLF
25	0	4317	7235	2010	0.007	115	22	13	MDW
26	75	3845	7669	2650	0.002	111	1	12	CBF
27	89	583	4785	979	0.003	114	30	17	CBF
29	0	4979	2628	527	0.002	101	11	10	MDW
31	31	2407	4045	2462	0.003	94	7	10	BPF
32	59	2031	4184	2643	0.002	97	40	11	CBF
33	0	1578	8597	2016	0.004	85	19	11	WTR
34	0	4113	2768	2100	0.035	87	6	12	EOF
35	79	1169	2830	1358	0.036	86	27	14	EOF
37	12	1756	9264	1875	0.004	84	33	10	MCF

reference category for LULC, with other classes coded as dummy variables (Downey, 2021). Other classes were Chirpine Forest, Cool Broadleaved Forest, Evergreen Oak Forest, Fir Forest, Hemlock Forest, Meadows, Mixed Conifer, and Waterhole.

Continuous variables were z-standardised (mean = 0, SD = 1). Collinear variables such as aspect, elevation and distance to drainage with a variance inflation factor [VIF] > 5 or correlation $|r| > 0.8$ were excluded (Kalnins & Praitis Hill, 2025).

Occupancy Modelling

A hierarchical Bayesian MSOM was fitted in PyMC version 5 (Downey, 2021). Continuous parameters were sampled with the No-U-Turn Sampler (NUTS); latent occupancy indicators z were modelled as Bernoulli variables. Species-specific occupancy probabilities (Ψ) were modelled as functions of site covariates, and detection probabilities (ρ) as functions of site and occasion covariates with season-specific intercepts. Closure was assumed for each 7-day occasion, and false positive error was considered negligible owing to species-level photo confirmation (Devarajan et al., 2020). Twelve chains were run with 10,000 warm-up iterations and 10,000 posterior draws (target_accept = 0.98; max_treedepth = 18). Convergence was assessed using trace plots, Gelman–Rubin diagnostics ($\hat{R} \leq 1.01$), and large effective sample sizes (minimum ESS_{bulk} : α = 34,554; β = 40,376; $\mathcal{E}$ = 41,410; Y_{num}= 47,363; Y_{lulc}= 118,619). Posterior predictive checks (PPCs) and Brier scores were used to evaluate model fit (Amir et al., 2022).

Spatial Prediction and Connectivity Modelling

Prey occupancy was projected onto a 500 × 500 m grid covering BC7 (N = 1,689) following Dickson et al. (2019) and Downey (2021). Prediction covariates were prepared using the same QGIS steps as for camera stations. Numeric covariates were z-standardised to training-set means (102.47, 43.03, 2661.39, 178.53, 3410.64, 1369.75, 186.92) and SDs (16.59, 40.13, 644.96, 81.81, 2108.33, 887.23, 132.77).

Posterior mean occupancy (ψ) in each cell was used as conductance, with values min-max scaled to [0,1]. ψ already lies in [0,1], so min–max scaling does not change the underlying information; it preserves the spatial ranking and relative contrasts while mapping values onto the conductance scale. Under this mapping, conductance magnitudes represent relative movement potential (not absolute rates). Resistance was defined as a $R = \frac{1}{C + \varepsilon}\ with\, \varepsilon = 10^{-6}$ where $\mathcal{E}$ represents a small constant (van Etten, 2017). Core cells were defined as high-use habitat ($\psi \geq 70$ %) and grouped using an 8-neighbour rule to form core patches. Centroids were partitioned into two terminal sets through k-means (k = 2). Random-walk connectivity (current density) between terminal sets was computed with *gdistance* (R package) (van Etten, 2017).

To create a community surface without dominance by any single species, species-specific current (passage) rasters were first normalised to 0–1 within species and then summed (van Etten, 2017). This harmonises dynamic range across species (equal weighting) while preserving within-species spatial rankings; consequently, the multi-species map is a relative index of passage intensity. Pinch points were defined as choke areas (cells ≥ 95th percentile of the multi-species passage surface), polygonised, filtered to remove parts < 0.25 km², and merged using a 1.5 km buffer to form macro zones. Resulting macro zones (M1–M7) were ranked by area (Dickson et al., 2019).

Results and Discussion

Sampling Effort and Model Performance

Thirty-one camera stations recorded 5,144 trap days and 822 independent events (mean: 166 trap days and 26 events per station). Generalists accounted for most detections (IE = 152–396), while specialists registered 21–33 events.

The MSOM showed excellent convergence (max $\hat{R} = 1.00$; min ESS_{bulk} = 34,554; min

$\mathrm{ESS}_{\mathrm{tail}} = 47{,}799$; 240,000 iterations; target_accept = 0.98; max_treedepth = 18). Overall model fit was strong (Brier score = 0.0553). Predicted detection probabilities spanned 0.013–0.320 across 18 species–season strata (6 species × 3 seasons). Mean occupancy across 186 site–species cells (31 sites × 6 species) was 0.548 (SD 0.303). Posterior predictive checks (faceted detection-rate PPCs) showed close agreement between predicted and observed means across species and seasons (Figure 2). These metrics support the use of an MSOM framework as a reliable tool to assess corridor function from camera trap data (Downey, 2021).

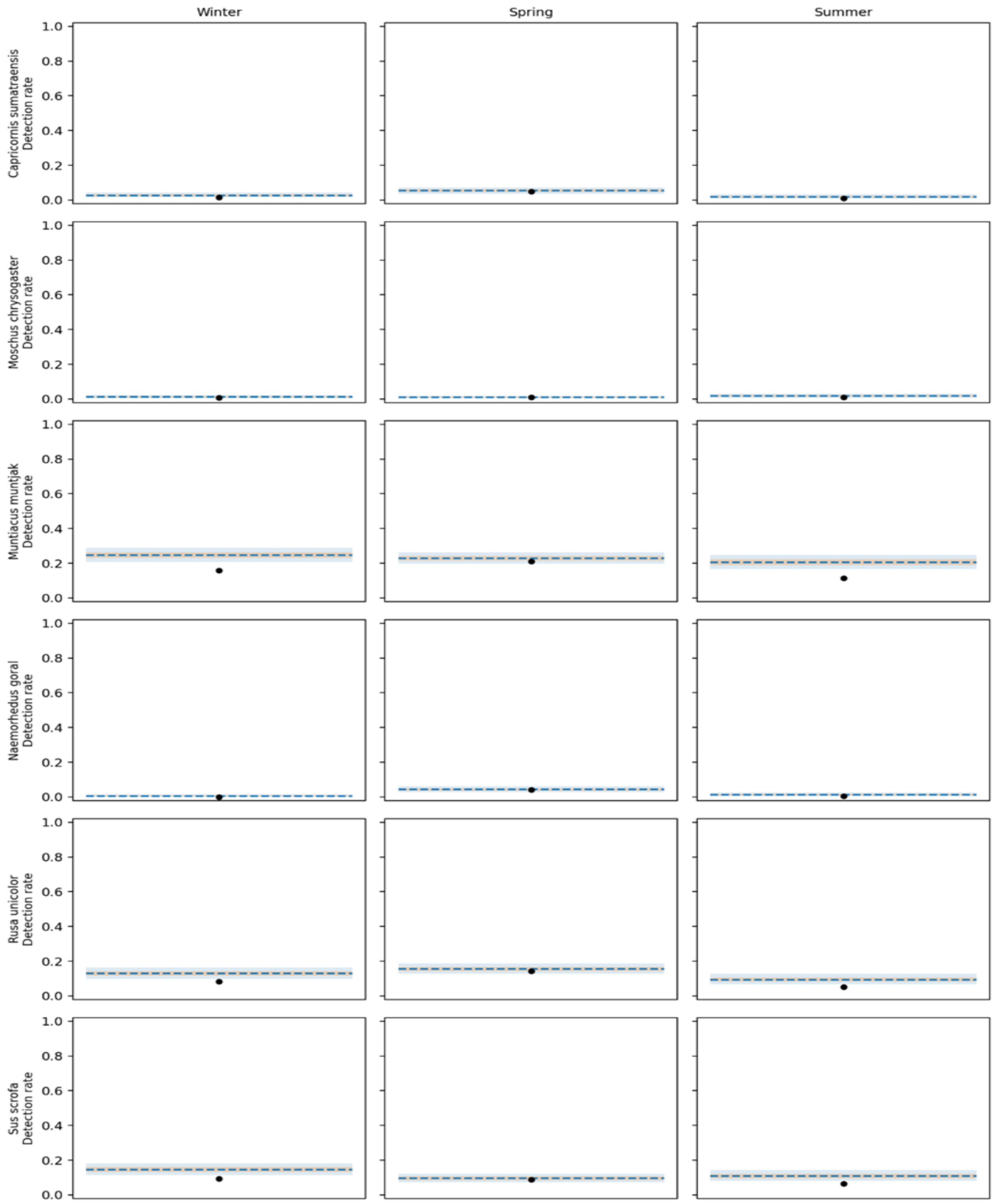

Figure 2: Posterior predictive checks (PPCs) for mean detection rates by species and season. Shaded bands: 50% and 95% posterior intervals; points: observed means. Most cells fall within 50%, all within 95%.

Prey Occupancy and Hotspots

Occupancy estimates across 31 camera stations differed markedly between generalists and specialists (Table 2). Barking deer exhibited near-ubiquitous occupancy (max $\psi = 0.99$ at CS09), with wild pig slightly lower (max $\psi = 0.94$ at CS11). Sambar deer reached $\psi = 0.98$ at CS20 with lower occupancy at higher elevations ($\psi = 0.07$ at CS14). Specialists were patchier. Himalayan serow peaked at CS13 ($\psi = 0.90$ at 3,218 m), musk deer at CS14 ($\psi = 0.65$ at 3,687 m) and Himalayan goral at CS37 ($\psi = 0.87$, 3,281 m). Minimum occupancy estimates for specialists were extremely low ($\psi = 0.01$–0.14), reflecting small, isolated pockets.

Letro et al. (2021) reported lower occupancy estimates ($\psi < 0.52$) for three ungulates (barking deer, wild pig and sambar deer), compared to higher estimates of generalists in BC7 ($\psi = 0.53$–0.62). These higher estimates are likely to reflect the suitability and minimal disturbance within BC7. However, differences in design and covariates should be taken into account when making comparisons across corridors.

Seasonal Detection and Behavioral Insights

Detection probabilities varied by species and season (Figure 3). Generalists exhibited higher detection ($\bar{p}= 0.2$) than specialists ($\bar{p} = 0.11$). Barking deer and wild pigs were most detectable in winter ($\bar{p}= 0.26$) and least detectable in summer ($\bar{p}= 0.23$), consistent with seasonal behaviours such as foraging and movement on open trails. Specialists were nearly absent in winter but peaked in spring ($\bar{p}= 0.10$ for Himalayan goral and serow), likely due to snowmelt and the emergence of the early herbaceous growth as seen in camera stations. Musk deer was an exception among specialists, remaining relatively stable across seasons ($p = 0.20$). The lower detection probability in summer is likely attributable to increased human and cattle activity as seen in the camera trap records.

Climatic and Anthropogenic Effects on Prey Occupancy

Most covariate coefficients had credible intervals overlapping zero, indicating uncertain effects on occupancy (Figure 4). One notable exception was the Himalayan serow, for which occupancy declined with increasing distance to roads ($\beta = -1.54$, logit scale, 95% *HDI* −2.84 to −0.26), implying higher occupancy closer to roads. This seemingly counterintuitive result may reflect localised attraction to roadside grazing edges along ridgelines. However, many studies indicate that roads reduce wildlife abundance through mortality, edge effects and noise (Lounsbury, 2025; Shi et al., 2018; Soanes et al., 2024). Accordingly, roads should not be interpreted as beneficial. Instead, targeted mitigation near roadside detections is warranted. Other covariates, such as canopy cover, slope and HFI, had wide credible intervals (*HDI* −2.47–2.04), suggesting

Table 2: Prey occupancy (ψ) across 31 camera stations. CS = Camera Station

Species	**Category**	**Min ψ**	**Station (elevation m)**	**Max ψ**	**Station (elevation m)**
Barking deer	Generalist	0.23	CS14 (3,687)	0.99	CS09 (2,150)
Sambar deer		0.07	CS14 (3,687)	0.98	CS20 (2,132)
Wild pig		0.22	CS03 (861)	0.94	CS11 (2,885)
Himalayan goral	Specialist	0.14	CS10 (2,149)	0.87	CS37 (3,281)
Himalayan serow		0.11	CS20 (2,132)	0.9	CS13 (3,218)
Musk deer		0.01	CS20 (2,132)	0.65	CS14 (3,687)

ungulate distributions are shaped by a complex interplay of habitat structure and human disturbance (Penjor, 2022).

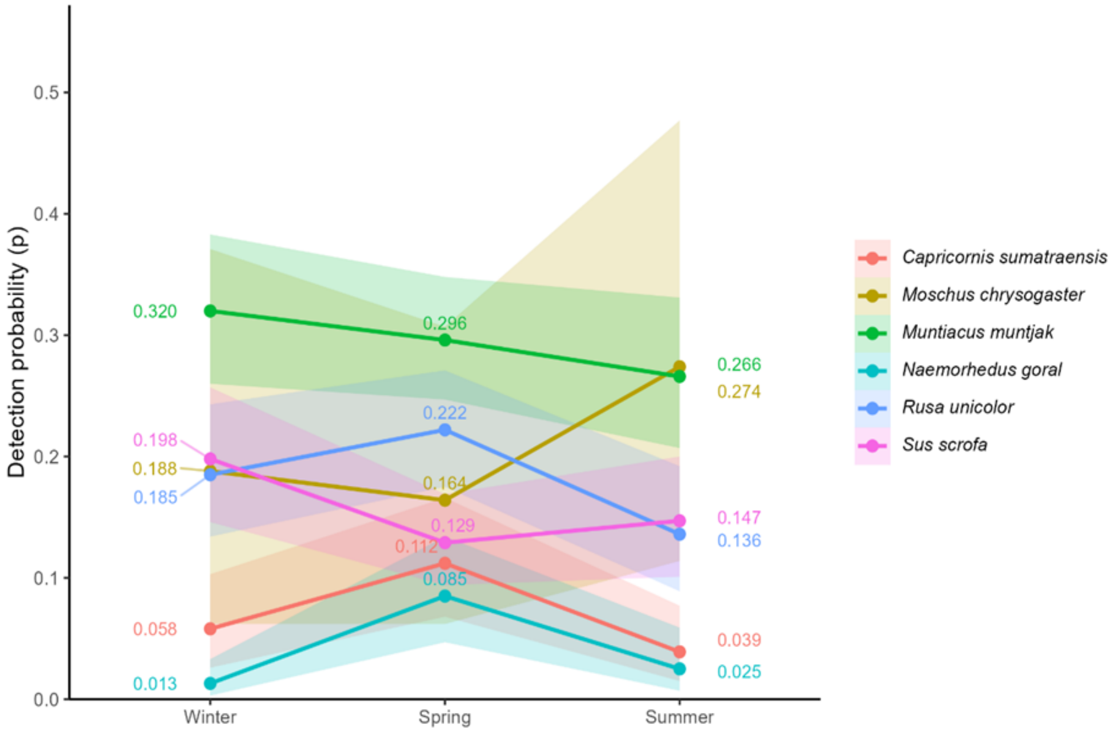

Figure 3: Seasonal detection probability (p) for prey species with 95% highest density intervals

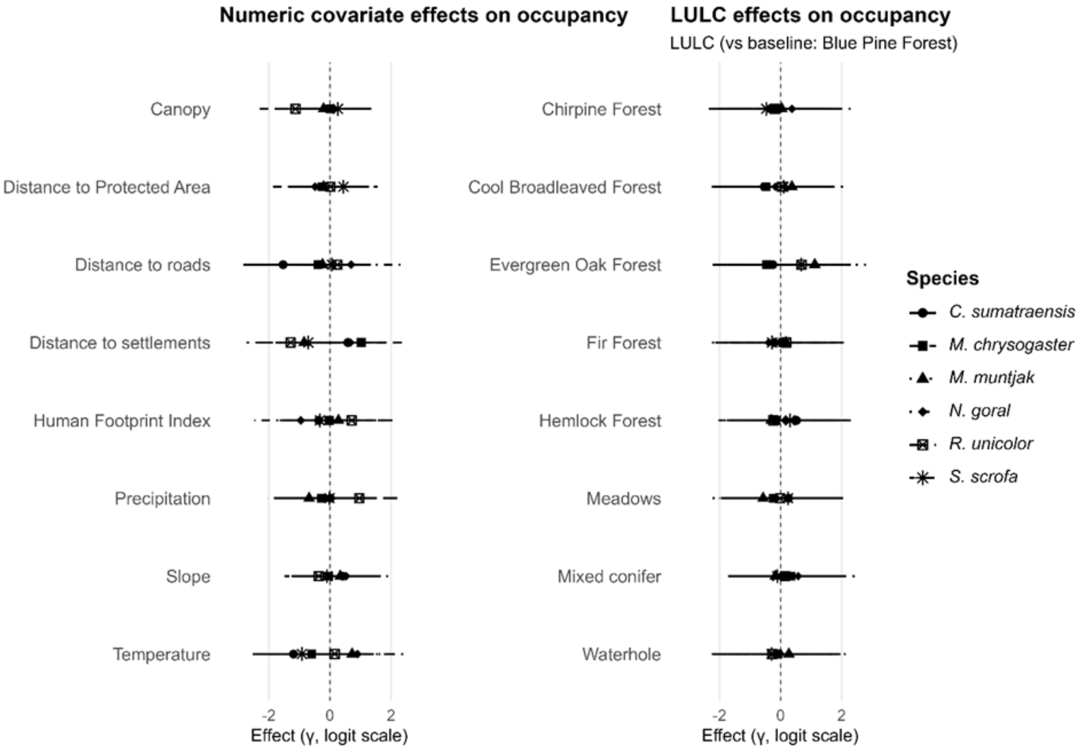

Figure 4: Posterior mean coefficients (points) with 95% highest density intervals (*HDI* bars) for numeric and categorical (LULC) covariates influencing prey occupancy (ψ)

Predicted Occupancy and Movement Corridors

Barking deer reached $\psi \geq 0.70$ in about 88 % of cells, sambar deer and wild pig showed similarly broad coverage, while specialists used only 20 to 40 % of cells, mostly in Blocks 1 and 2, with musk deer absent from Block 3. The result accords with prior work: barking deer and wild pig behave as edge-tolerant generalists; sambar deer tend to decline in steep, high-elevation terrain; and serow, goral and musk deer are associated with steep slopes and conifer forests (Dorji et al., 2019; Letro et al., 2021; Penjor, 2022). These spatial predictions align with station-level occupancy (Table 2) and suggest that management should prioritise high-elevation refugia and mid-elevation riparian corridors.

Seven macro pinch point zones (M1 to M7) totalling about 152 km² were identified primarily in Blocks 1 and 2 (Figure 5). These zones represent key movement corridors or bottlenecks where movement is constrained and directed by topography, habitat quality, and the placement of roads and rivers. Corridors used by specialists may be particularly sensitive to modelling design and imperfect detections. Therefore, further validation is recommended before concluding. This includes adding seasons and, where feasible, using telemetry or genetic data (Dhendup et al., 2023; Tempa, 2017).

Wildlife Conflicts Segments and Mitigation Options

Pinch point polygons buffered by 100 m and intersected with infrastructure produced 29 road conflict segments (total length: 29.8 km) and 18 river conflict segments (total length: 11.6 km; Figure 6). Many segments were less than 500 m, with 35 % of road segments and 53 % of river segments below that length, which indicates that modest widening or embankment works could sever connectivity if not mitigated. The top ten candidates accounted for 12.2 km of roads and 11.5 km of rivers.

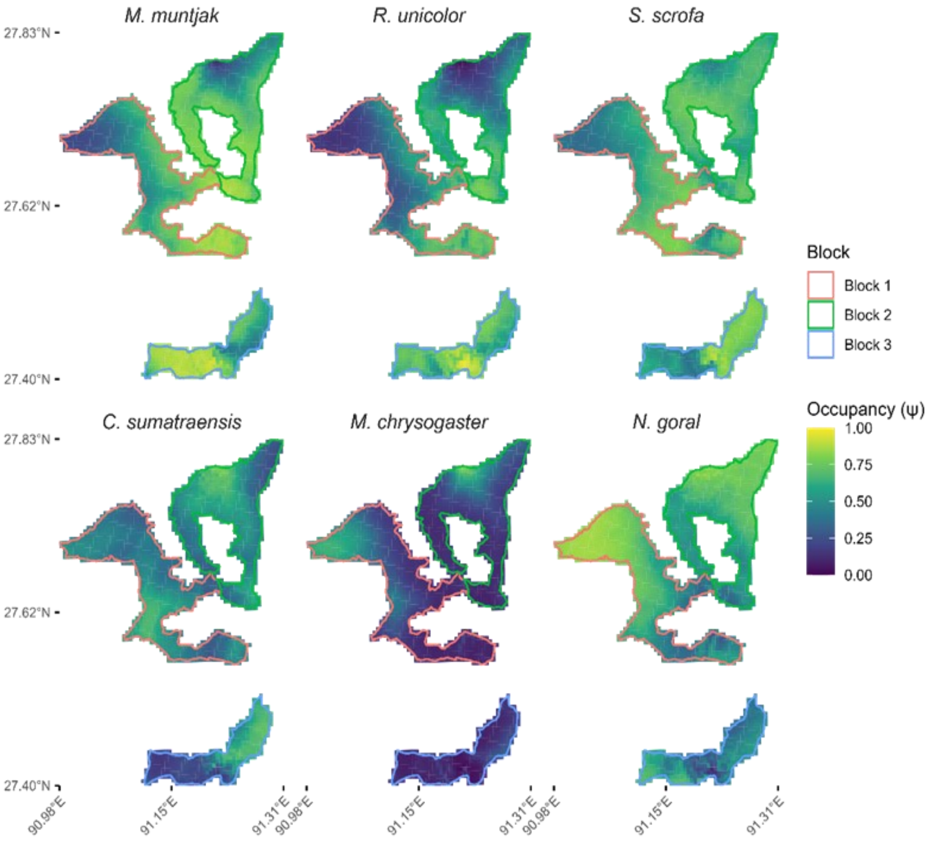

Figure 5: Predicted occupancy ($\psi \geq 0.7$) of prey species across a 500 m^2 grid ($N = 1689$ cells)

Mitigation options included bridge-style underpasses or culverts at riparian conflicts, vegetated overpasses on dry slopes, continuous exclusion fencing paired with speed reduction, and riparian canopy buffers. As Rautela et al. (2022) and Soanes et al. (2024) showed, combining overpasses or underpasses with fencing can restore a large share of connectivity when designs match local terrain and target species, which aligns with findings of Lounsbury (2025) and Shi et al. (2018).

Planning Framework and Evidence Thresholds

Bhutan’s policy and practice indicate feasibility. WCD (2010) recognises wildlife-friendly linear infrastructure in corridor guidance, and the Asian Development Bank's (2022) project evaluations document the wildlife's use of new underpasses. However, given the six-month duration and the focus on six prey species, the pinch points can serve as an initial screening layer, not as a siting plan. They can guide field verification, multi-season surveys, and feasibility assessment, but they should not be the sole basis for locating wildlife crossings. For each candidate segment, pair the results with traffic counts and collision records from the relevant transport agencies and with local observations of river crossings during peak flows as suggested by Shi et al. (2018) and WCD (2010). If riparian works are considered along the Kurichhu, planning documents for the DHP project provide a coordination context for river segments (DGPCL, 2025). Effective mitigation should also balance connectivity with livelihoods through careful placement of crossing structures and community-led monitoring and maintenance, which is important because more than 190 households live within the corridor (DFOM, 2023).

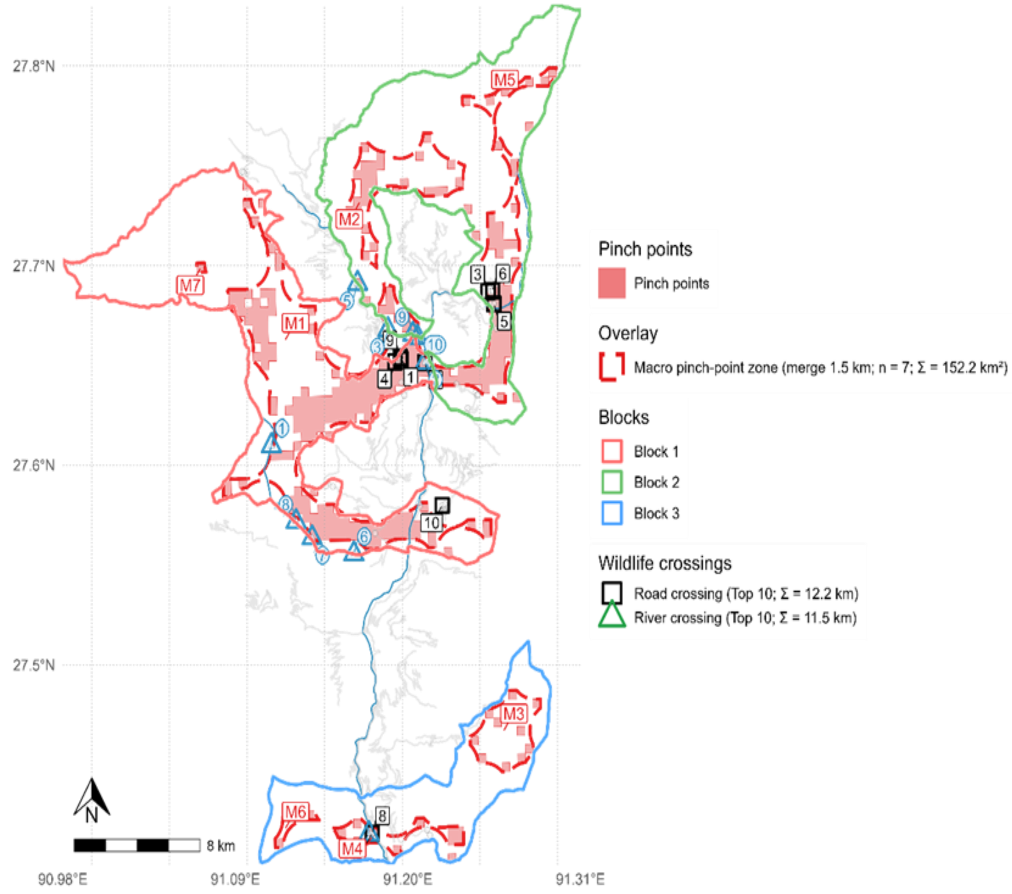

Figure 6: Pinch points and proposed wildlife crossings along roads and rivers in BC7

Implications for Predators and Climate Adaptation

A tiger was recorded at two stations in Block 2 at elevations of 2,352 m and 2,687 m, indicating the use of BC7 by an apex predator and likely indicating its movement between BWS and WCNP. However, the movement of tigers between these protected areas should be further validated by telemetry or genetic studies (Dhendup et al., 2023; Tempa, 2017). From prey's perspective, the high occupancy of generalist prey suggests that BC7 currently facilitates tiger dispersal between protected areas. However, the narrow, elevation-restricted routes used by specialists may constrain predator access to high-elevation habitats. As the rise in temperature drives species to higher elevations and human development intensifies, protecting elevational gradients and riparian corridors becomes even more important (Deka et al., 2023; Lee et al., 2021). With Bhutan's national tiger survey reporting 131 wild tigers in 2021–2022 (DoFPS, 2023), maintaining prey-rich corridors is critical for sustaining meta-population connectivity.

Study Limitations and Future Directions

This study drew on 31 stations over six months, focusing on prey species and using the random walk connectivity model as a proxy for movement. Therefore, seasonal dynamics, community (predator-prey relationship) structure, and fine-scale behaviour may be underrepresented. Future studies could extend sampling into late summer and autumn, incorporate telemetry or genetic data to validate connectivity models, test alternative connectivity algorithms, such as least-cost path or neural network approaches, and include predator species to evaluate community interactions, like the study carried out by Amir et al. (2022). Despite these limitations, the consistency of the model diagnostics and the alignment between station-level and grid-level results increase confidence in the identified movement hotspots. Pinch points identified here are a model-based screening layer rather than a siting plan; any wildlife crossing should be prioritised only after pairing candidate segments with traffic volumes and roadkill/conflict records. Designs should then be validated with before–and–after monitoring (camera traps, telemetry and incident logs).

Conclusion

Occupancy and connectivity analyses indicated that BC7 remains functionally important for both prey and predator movement between protected areas. Generalist ungulates showed high, widespread occupancy, suggesting strong baseline permeability, while specialists used narrow, high-elevation corridors vulnerable to fragmentation. By integrating MSOM with a connectivity model, this study delineated seven pinch point zones and prioritised road and river segments where mitigation would most effectively sustain ecological connectivity. These findings provide a defensible basis for locating wildlife crossings, fencing, and riparian buffers as infrastructure expands. Proactive investment in corridor mitigation and continued monitoring will be essential to maintain BC7's ecological function under increasing climate pressure and developmental activities. Overall, this study demonstrates how combining MSOM with a connectivity model can translate camera-trap data into actionable corridor management. Next steps should include predator-focused occupancy and independent movement evidence (e.g., telemetry or genetic assignment) to validate and refine priorities, alongside comparable corridor-scale studies elsewhere in Bhutan to build a consistent evidence base.

Acknowledgment

This research supports decision-making for Biological Corridor 7 under emerging infrastructure and climate challenges. The authors express gratitude to Royal Government of Bhutan, Royal Civil Service Commission, Department of Forests and Park Services, Royal

University of Bhutan, College of Natural Resources and Mongar Forest Division for their administrative support. Sincere thanks are extended to UNESCO Madanjeet Centre for South Asian Forestry Studies (MCSAFS), Mohamed bin Zayed Species Conservation Fund, Bhutan Ecological Society, and Bhutan Trust Fund for Environmental Conservation for generously funding data collection. Heartfelt gratitude is expressed to Nature Conservation Division for providing camera traps, without which this study would not have been possible.

References

Adhikari, J. N., Bhattarai, B. P., Baral, S., & Thapa, T. B. (2024). Landscape-level habitat connectivity of large mammals in Chitwan-Annapurna Landscape, Nepal. *Ecology and Evolution*. https://doi.org/10.1002/ece3.70087

Ahmad, A., & Gopi, G. V. (2024). Site occupancy of select mammals in the tropical forest of Eastern Himalaya. *Frontiers in Ecology and Evolution*. https://doi.org/10.3389/fevo.2023.1106329

Amir, Z., Sovie, A., & Luskin, M. S. (2022). Inferring predator–prey interactions from camera traps: A Bayesian co-abundance modeling approach. *Ecology and Evolution*, *12*(12). https://doi.org/10.1002/ece3.9627

Bowman, J., Adey, E., Angoh, S. Y. J., Ethier, D. M., Gauthier, J., Iwanycki, N. E., & Wilson, P. J. (2020). Effects of cost surface uncertainty on current density estimates from circuit theory. *PeerJ*, *8*, e9617. https://doi.org/10.7717/peerj.9617

Deka, J. R., Ali, S. Z., Ahamad, M., Borah, P., Gopi, G. V., Badola, R., Sharma, R., & Hussain, S. A. (2023). Can Bengal Tiger (Panthera tigris tigris) endure the future climate and land use change scenario in the East Himalayan Region? Perspective from a multiple model framework. *Ecol Evol*, *13*(8), e10340. https://doi.org/10.1002/ece3.10340

Department of Forests and Park Services. (2023). *Status of tigers in Bhutan: The National Tiger Survey Report 2021–2022*. Bhutan Tiger Center, Ministry of Energy and Natural Resources, Thimphu, Bhutan.

Department of Forests and Park Services. (2024). *Annual Forestry Statistics 2023*. Forest Monitoring and Information Division, Ministry of Energy and Natural Resources, Thimphu, Bhutan.

Devarajan, K., Morelli, T. L., & Tenan, S. (2020). Multi-species occupancy models: review, roadmap, and recommendations. *Ecography*, *43*(11), 1612-1624. https://doi.org/10.1111/ecog.04957

Dickson, B. G., Albano, C. M., Anantharaman, R., Beier, P., Fargione, J., Graves, T. A., Gray, M. E., Hall, K. R., Lawler, J. J., Leonard, P. B., Littlefield, C. E., McClure, M. L., Novembre, J., Schloss, C. A., Schumaker, N. H., Shah, V. B., & Theobald, D. M. (2019). Circuit-theory applications to connectivity science and conservation. *Conservation Biology*, *33*(2), 239-249. https://doi.org/10.1111/cobi.13230

Divisional Forest Office of Mongar. (2023). *Conservation Management Plan for Biological Corridor 07 (Connecting PNP-BWS-WCNP) Jan 2023 - December 2032*. Divisional Forest Office of Mongar, Department of Forests and Park Services, Mongar, Bhutan.

Dorji, S. (2019). *Mapping Conservation Priorities and Assessing Connectivity Pathways for Threatened Mammals under Changing Climate and Land-use in the Eastern Himalayas* (Master's thesis, University of New England, Armidale, NSW, Australia). University of New England.

Downey, A. B. (2021). *Bayesian Inference with PyMC*. Retrieved August 16, 2025, from https:// allendowney.github.io/BayesianInferencePyMC/index.html

Druk Green Power Corporation Limited. (2025). *Environment & Social Management Plan (ESMP): 1125 MW Dorjilung Hydropower Project (DHPP), Mongar and Lhuentse, Bhutan — Draft*. Druk Green Power Corporation Limited, Thimphu, Bhutan.

Forest Resource Management Division. (2019). *Forest cover loss from three hydropower projects (Punatsangchhu-I, Punatsangchhu-II, and Mangdechhu Hydroelectric Project Authorities) and their corresponding transmission lines*. Department of Forests and Park Services, Thimphu, Bhutan.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*, *342*(6160), 850-853. https://doi.org/10.1126/science.1244693

Hausfather, Z. (2025, 2025-01-10). State of the climate: 2024 sets a new record as the first year above 1.5°C. *Carbon Brief*. https://www.carbonbrief.org/state-of-the-climate-2024-sets-a-new-record-as-the-first-year-above-1-5c/

Hawker, L., Uhe, P., Paulo, L., Sosa, J., Savage, J., Sampson, C., Neal, J., & Bates, P. (2022). A 30 m global map of elevation with forests and buildings removed. *Environmental Research Letters*, *17*(2), 024016. https://doi.org/10.1088/1748-9326/ac4d4f

Hilty, J., Worboys, G. L., Keeley, A., Woodley, S., Lausche, B., Locke, H., Carr, M., Pulsford, I., Pittock, J., White, J. W., Theobald, D. M., Levine, J., Reuling, M., Watson, J. E. M., Ament, R., & Tabor, G. M. (2020). *Guidelines for conserving connectivity through ecological networks and corridors*. IUCN. https://doi.org/10.2305/IUCN.CH.2020.PAG.30.en

Huynh, H.-D., Schofield, M., & Hwang, W.-H. (2024). Site occupancy and abundance models for analyzing multiple-visit detection/nondetection data. *The Annals of Applied Statistics*, *18*(3), 2424-2443.

Kalnins, A., & Praitis Hill, K. (2025). The VIF score. What is it good for? Absolutely nothing. *Organizational Research Methods*, *28*(1), 58-75.

Lee, J.-Y., Marotzke, J., Bala, G., Cao, L., Corti, S., Dunne, J. P., Engelbrecht, F., Fischer, E., Fyfe, J. C., Jones, C., Maycock, A., Mutemi, J., Ndiaye, O., Panickal, S., & Zhou, T. (2021). Future Global Climate: Scenario-based Projections and Near-term Information. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 553-672). Cambridge University Press. https://doi.org/10.1017/9781009157896.006

Letro, L., Fischer, K., Duba, D., & Tandin, T. (2021). Occupancy patterns of prey species in a biological corridor and inferences for tiger population connectivity between national parks in Bhutan. *Oryx*, *56*(3), 421-428. https://doi.org/10.1017/s0030605320000976

Lounsbury, S. (2025). *Evaluating the effectiveness of an innovative road mortality mitigation design for at-risk reptiles in eastern Georgian Bay, Ontario* (Doctoral Dissertation).

Meyer, N. F. V., Moreno, R., Reyna-Hurtado, R., Signer, J., & Balkenhol, N. (2020). Towards the restoration of the Mesoamerican Biological Corridor for large mammals in Panama: comparing multi-species occupancy to movement models. *Movement Ecology*, *8*, 1-14. https://doi.org/10.1186/s40462-019-0186-0

National Centre for Hydrology and Meteorology. (2025). *Rainfall and temperature forecast of Bhutan for Summer Monsoon (June–September 2025)*. Meteorological Services Division, Thimphu, Bhutan.

OpenStreetMap, c. (2025). *OpenStreetMap*. OpenStreetMap Foundation. https://www.openstreetmap.org

Qgis.org. (2024). *QGIS Geographic Information System*. In (Version 3.40) [Computer software]. QGIS Association. https://qgis.org

Rai, A. (2022). *Forest Types of Bhutan* [GIS dataset]. Department of Forests and Park Services, Royal Government of Bhutan, Thimphu, Bhutan.

Rai, A., Phuntsho, P., & Tshering, C. (2021). *Land Use and Land Cover Assessment of Bhutan 2016* [GIS dataset]. Department of Forests and Park Services, Royal Government of Bhutan, Thimphu, Bhutan.

Rautela, N., Shanu, S., Agarwal, A., Bhattacharya, S., & Roy, A. (2022). Geospatial modelling of overlapping habitats for identification of tiger corridor networks in the Terai Arc landscape of India. *Geocarto International*, *37*(27), 15114-15142. https://doi.org/10.1080/10106049.2022.2095444

Scotson, L., Johnston, L. R., Iannarilli, F., Wearn, O. R., Mohd-Azlan, J., Wong, Wai M., Gray, T. N. E., Dinata, Y., Suzuki, A., Willard, C. E., Frechette, J., Loken, B., Steinmetz, R., Moßbrucker, A. M., Clements, G. R., Fieberg, J., Rowcliffe, M., & De Angelo, C. (2017). Best practices and software for the management and sharing of camera trap data for small and large scales studies. *Remote Sensing in Ecology and Conservation*, *3*(3), 158-172. https://doi.org/10.1002/rse2.54

Scott, C. M. (2021). *Robust Assessment of Changes in Wild Mammal Occupancy and Activity Relative to Livestock and Human Disturbance* (Master's thesis, Trent University, Environmental and Life Sciences, Peterborough, Ontario, Canada). Trent University Graduate Thesis Collection.

Shi, H., Shi, T., Yang, Z., Wang, Z., Han, F., & Wang, C. (2018). Effect of Roads on Ecological Corridors Used for Wildlife Movement in a Natural Heritage Site. *Sustainability*, *10*(8). https://doi.org/10.3390/su10082725

Singh, P. B., Saud, P., Cram, D., Mainali, K., Thapa, A., Chhetri, N. B., Poudyal, L. P., Baral, H. S., & Jiang, Z. (2019). Ecological correlates of Himalayan musk deer *Moschus leucogaster*. *Ecology and Evolution*, *9*(1), 4-18. https://doi.org/10.1002/ece3.4435

Soanes, K., Rytwinski, T., Fahrig, L., Huijser, M. P., Jaeger, J. A. G., Teixeira, F. Z., van der Ree, R., & van der Grift, E. A. (2024). Do wildlife crossing structures mitigate the barrier effect of roads on animal movement? A global assessment. *Journal of Applied Ecology*, *61*(3), 417-430. https://doi.org/10.1111/1365-2664.14582

Thapa, K., Subba, S. A., Thapa, G. J., Dewan, K., Acharya, B. P., Bohara, D., Subedi, S., Karki, M. T., Gotame, B., Paudel, G., Bhatta, S. R., Jnawali, S. R., & Malla, S. (2022). Wildlife in climate refugia: Mammalian diversity, occupancy and tiger distribution in the Western Himalayas, Nepal. *Ecology and Evolution*. https://doi.org/10.1002/ece3.9600

Thinley, P., Dendup, T., Rajaratnam, R., Vernes, K., Tempa, K., Chophel, T., & Norbu, L. (2020). Tiger reappearance in Bhutan's Bumdeling Wildlife Sanctuary: a case for maintaining effective corridors and metapopulations. *Animal Conservation*, *23*(6), 629-631.

van Etten, J. (2017). R package gdistance: Distances and routes on geographical grids. *Journal of Statistical Software*, *76*(13), 1-21. https://doi.org/10.18637/jss.v076.i13

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. M. (2016). Global terrestrial Human Footprint maps for 1993 and 2009. *Scientific Data*, *3*, 160067. https://doi.org/10.1038/sdata.2016.67

Wangchuk, T. (2004). *A Field Guide to the Mammals of Bhutan*. Department of Forestry, Ministry of Agriculture, Royal Government of Bhutan, Thimphu, Bhutan.

Westcott, J. (2024). *Modelling current and projected niche shifts of the blacklegged tick, Ixodes scapularis, in eastern Canada employing community science data and global climate change drivers* (Master's thesis, Memorial University of Newfoundland, Grenfell Campus, Corner Brook, NL, Canada). Memorial Scholaris.