# Movement states and seasonal search dynamics of GPS-collared Asian elephants in a Himalayan foothills

## Abstract

*Resource seasonality can reshape the movement tactics of wide-ranging herbivores, particularly in fragmented foothills where forest, riparian habitat, agricultural edges, and settlements occur in close proximity. GPS telemetry from four collared Asian elephants (Elephas maximus) in the Gelephu-Sarpang region of south-central Bhutan was used to evaluate seasonal movement-state allocation, movement clustering, vegetation greenness, and seasonal space use. A three-state movement model classified 39,566 steps into resting-like, foraging-like, and travelling-like states inferred from step length and turning angle. Travelling-like movement accounted for the largest overall share of fixes (48.0%), followed by foraging-like (27.7%) and resting-like (24.2%) states, with substantial individual variation. First-passage time (FPT) analysis identified movement clustering at radii of 4,183-5,000 m and seven candidate area-restricted search (ARS) zones. Three individuals reached the 5,000 m upper radius limit, so those ARS scales represent lower-bound estimates within the tested range. MODIS NDVI phenology indicated strong seasonal greenness variation across the study area (mean NDVI = 0.657; mean amplitude = 0.786; mean CV = 26.9%), but NDVI was treated strictly as a greenness proxy rather than a direct measure of forage quality or intake. Seasonal KDE estimates showed dry-season expansion of 95% ranges, most strongly for GMC_04 (347.8 km2 dry season vs. 123.7 km2 monsoon). Exploratory anomaly screening identified 3,729 statistical outliers (9.4% of fixes), while the isolation forest component flagged 1,979 fixes. These results identify candidate monitoring and validation areas where movement clustering, dry-season expansion, shared seasonal space use, and unusual movement records can be evaluated with field data.*

**Keywords:** behavioural ecology; hidden Markov model; first-passage time; area-restricted search; NDVI; seasonal home range; anomaly screening; Asian elephant; *Elephas maximus*; Bhutan

## Introduction

Animal movement links individual behaviour to spatially and temporally variable environments. For large herbivores, seasonal variation in forage, water, crop availability, and human activity can alter movement-state allocation, search intensity, and seasonal range configuration. These processes are especially important for Asian elephants (*Elephas maximus*) in Himalayan foothill regions, where seasonal movements occur within fragmented landscapes that include forests, riverine habitat, agricultural margins, settlements, and transboundary movement routes.

GPS telemetry permits continuous movement analysis, but movement metrics do not directly observe behaviour. Hidden Markov models and related movement-state classifiers infer latent states from step lengths and turning angles (Patterson et al., 2009; McClintock & Michelot, 2020). State labels such as resting-like, foraging-like, and travelling-like therefore describe movement signatures rather than confirmed behavioural observations. First-passage time analysis provides a complementary estimate of the spatial scale at which an animal's trajectory becomes locally clustered, a pattern commonly interpreted as area-restricted search (Fauchald & Tveraa, 2003). ARS indicates movement concentration and possible search behaviour, but independent field evidence is required before assigning ecological function to a clustered location.

Vegetation phenology provides the seasonal environmental context for movement interpretation. NDVI is a long-established spectral index for photosynthetically active vegetation (Tucker, 1979), and satellite-derived NDVI has been widely used to evaluate ecological responses to environmental variability (Pettorelli et al., 2005). MODIS vegetation-index products provide regular, broad-extent greenness observations suitable for landscape-scale phenology summaries (Huete et al., 2002; Didan, 2021). However, NDVI does not measure forage species composition, digestibility, water availability, crop use, or intake. Seasonal home-range estimates can describe spatial expansion and centroid shifts, although conventional KDEs remain descriptive under high-frequency, autocorrelated telemetry (Fleming et al., 2015; Noonan et al., 2019). These methods are most informative when interpreted together and with explicit limits on inference.

The central question addressed here is: how do GPS-collared Asian elephants modulate movement state, search intensity, and seasonal space use in response to resource seasonality in a fragmented Himalayan foothill region? The analysis combines movement-state classification, FPT-based movement clustering, NDVI phenology, seasonal KDE, pairwise seasonal-polygon overlap, and exploratory anomaly screening. Inference is restricted to the four tracked individuals and should not be generalized to the species or regional population without additional collars and field validation.

## Methods

### *Study area*

The study was conducted in the Gelephu, Sarpang and adjoining Indian plains, a Himalayan foothill landscape characterized by a heterogeneous mosaic of subtropical forests, riparian habitats, agricultural land, and human settlements. The region experiences strong seasonal variation, with a monsoon season (May–October) characterized by high precipitation and vegetation productivity, and a dry season (November–April) associated with reduced water availability and lower primary productivity. The region functions as a critical movement pathway for elephants, linking protected areas and facilitating transboundary movement.

### *GPS collar data*

Four adult Asian elephants (Elephas maximus) were fitted with GPS collars (GMC_01–GMC_04) and monitored at 10-minute intervals. After data cleaning and quality control, a total of 39,578 validated fixes were retained for analysis. Tracking durations ranged from 328 to 545 days per individual. Movement trajectories were constructed from sequential fixes, and step lengths (m) and turning angles (radians) were calculated. All spatial data were projected to a UTM coordinate system (WGS84 / UTM Zone 45N) to ensure accurate distance calculations.

### *Environmental covariates*

Vegetation dynamics were quantified using MODIS MOD13Q1 NDVI data (250 m spatial resolution, 16-day temporal resolution) for the period 2020–2024. NDVI values were scaled using the standard MODIS factor (0.0001) and filtered to remove invalid observations (Didan, 2021).

For each GPS fix, NDVI values were extracted using spatial interpolation. Additional environmental covariates included:

- Distance to settlements (m)
- Distance to rivers (m)
- Elevation and terrain variables (derived from DEM)
- Seasonal classification (monsoon vs dry)

NDVI was treated as a proxy for vegetation greenness rather than direct forage quality.

### *Movement-state classification*

Movement states were inferred using Hidden Markov Models implemented in the R package momentuHMM. A three-state model was fitted to step lengths and turning angles using gamma and von Mises distributions, respectively.
To evaluate environmental influences on movement behaviour, state transition probabilities were modelled as functions of covariates:

- NDVI
- Season
- Distance to settlements

The transition probability between states was defined as:

$$\gamma ij(t) = \frac{(\boldsymbol{exp}(\beta ij,0 + \beta ij,1 \cdot NDVIt + \beta ij,2 \cdot Seasont + \beta ij,3 \cdot DistSettlet)}{(\sum \mathrm{k} exp(\beta \mathrm{ik},0 + \beta \mathrm{ik},1 \cdot \mathrm{NDVIt} + \cdots)}$$

Model selection was based on Akaike Information Criterion (AIC), and parameter uncertainty was evaluated using standard errors and confidence intervals.

### *First-passage time and movement clustering*

First-passage time (FPT) was used to identify spatial scales of movement clustering and candidate area-restricted search (ARS) behaviour following first-passage time. FPT was calculated across a range of radii (100–10,000 m), and the optimal radius was defined as the value maximizing variance in log-transformed FPT.

To evaluate environmental drivers of search behaviour, FPT values were modelled using generalized additive models (GAMs):

$log(\mathrm{FPT}) = s(\mathrm{NDVI}) + \mathrm{Season} + {}^{b}\mathrm{individual} + \epsilon$

where $s(\cdot)$ represents a smoothing function and $^{b}$individual is a random effect.

### *Seasonal home-range estimation*

Seasonal space use was quantified using autocorrelated kernel density estimation implemented in the R package *ctmm* (Fleming et al., 2015). AKDE accounts for temporal autocorrelation in movement data and provides statistically robust estimates of home-range area. Separate models were fitted for monsoon and dry seasons, and 95% utilization distributions were derived. Differences in home-range size between seasons were tested using paired comparisons across individuals.

### *Home-range overlap*

Overlap between individual home ranges was quantified using:

- Bhattacharyya’s affinity (BA)
- Utilization Distribution Overlap Index (UDOI)

These metrics were calculated from utilization distributions rather than polygon intersections, ensuring bounded and interpretable overlap estimates.

### *Movement–environment relationships*

To directly test environmental influences on movement states, a multinomial logistic regression framework was applied:

$$P(\text{State}i) = f(\text{NDVI}, \text{Season}, \text{DistSettle}) + (1|\text{Individual})$$

where individual identity was included as a random effect to account for repeated measures.

### *Anomaly detection and validation*

Movement anomalies were identified using an ensemble approach combining:

- Statistical outlier detection (z-score, IQR)
- Isolation Forest (scikit-learn)
- Rolling behavioural change metrics

To evaluate ecological drivers, anomaly occurrence was modelled as:

$$\text{Anomaly} \sim \text{NDVI} + \text{DistSettle} + \text{Season}$$

This allowed testing whether anomalies were associated with environmental or anthropogenic factors.

### *Software and reproducibility*

All analyses were conducted in R (version ≥4.3) and Python (version ≥3.10). Key packages included:

- *momentuHMM*
- *ctmm*
- *mgcv*
- *scikit-learn*

Reproducible workflows and run summaries were maintained within the project repository.

## Results

### *Movement states*

The movement-state workflow classified 39,566 valid steps. Travelling-like movement was the most common state overall (48.0%), followed by foraging-like (27.7%) and resting-like (24.2%) states (Table 1). Individual variation was pronounced: GMC_02 had the highest travelling-like proportion (61.6%), whereas GMC_03 had the highest foraging-like proportion (40.3%).

**Table 1.** Proportion of GPS fixes assigned to each movement-derived state by elephant. State labels describe inferred movement signatures, not directly observed behaviour.

| Elephant | Resting-like (n, %) | Foraging-like (n, %) | Travelling-like (n, %) |
|---|---|---|---|
| GMC_01 | 3,912 (26.2%) | 4,025 (26.9%) | 7,008 (46.9%) |
| GMC_02 | 1,627 (15.6%) | 2,378 (22.8%) | 6,428 (61.6%) |
| GMC_03 | 511 (22.9%) | 898 (40.3%) | 820 (36.8%) |
| GMC_04 | 3,541 (29.6%) | 3,671 (30.7%) | 4,747 (39.7%) |
| **Overall** | **9,591 (24.2%)** | **10,972 (27.7%)** | **19,003 (48.0%)** |

The corrected transition matrix indicated state persistence, especially for travelling-like movement ($P = 0.677$; Table 2). Transitions from resting-like to foraging-like movement ($P = 0.358$) and from foraging-like to travelling-like movement ($P = 0.353$) were also common.

**Table 2.** Corrected movement-state transition matrix from the repository HMM run summary. Rows indicate the starting state and columns indicate the next state.

| From -> To | Resting-like | Foraging-like | Travelling-like |
|---|---|---|---|
| Resting-like | 0.406 | 0.358 | 0.236 |
| Foraging-like | 0.270 | 0.377 | 0.353 |
| Travelling-like | 0.144 | 0.179 | 0.677 |

### *First-passage time and candidate ARS zones*

FPT analysis identified movement-clustering scales of 4,183-5,000 m (Table 3). GMC_01, GMC_02, and GMC_04 reached the 5,000 m upper radius limit, indicating that the selected scale for those individuals is censored by the radius range. GMC_03 had the highest FPT variance (261,226) at 4,183 m, indicating the strongest local clustering within the tested range.

**Table 3.** First-passage time analysis results. Radius values at 5,000 m are lower-bound estimates within the tested range.

| Elephant | Optimal Radius (m) | Max FPT Variance | Fixes Analyzed |
|---|---|---|---|
| GMC_01 | 5,000 | 110,303 | 14,948 |
| GMC_02 | 5,000 | 20,647 | 10,436 |
| GMC_03 | 4,183 | 261,226 | 2,232 |
| GMC_04 | 5,000 | 60,399 | 11,962 |

Seven candidate ARS zones were detected across all individuals. These zones represent movement concentration and are best interpreted as candidate locations for field validation of vegetation, water, crop access, terrain constraints, or human activity.

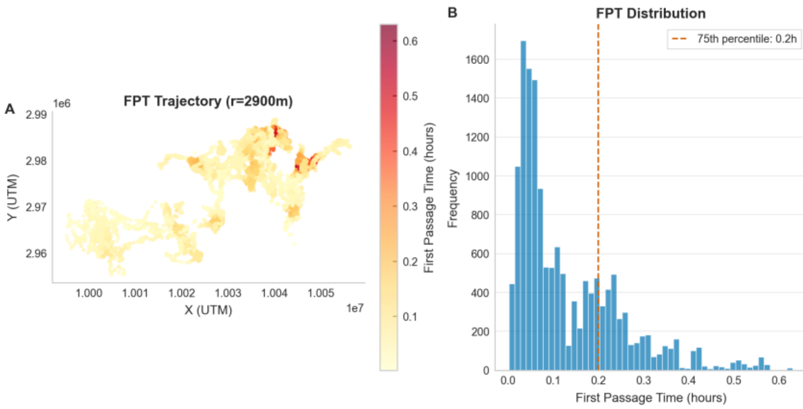


***Figure 1.*** *First-passage time trajectory for GMC_01. Colours represent first-passage time values at the tested 5,000 m radius and indicate movement clustering.*

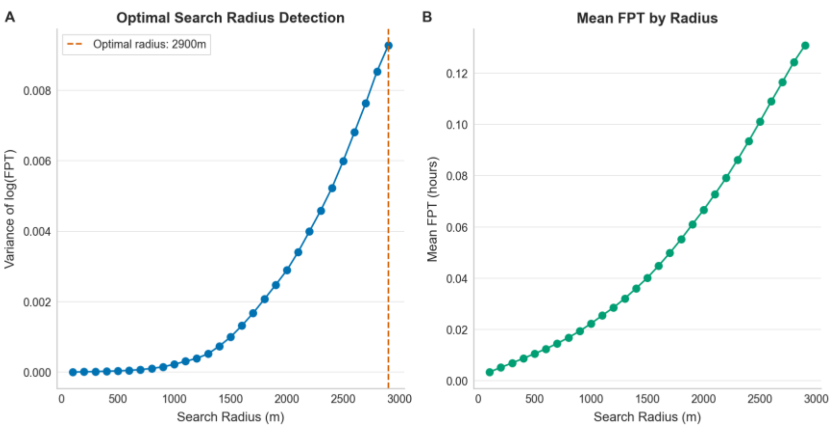


***Figure 2.*** *Radius-optimization curve for GMC_01. The variance peak occurs at the 5,000 m upper bound of the tested range, indicating a lower-bound movement-clustering scale in this workflow.*

### *NDVI phenology and movement-state context*

The MODIS NDVI phenology workflow showed strong seasonal greenness variation across the study area. The sampled phenology summary reported mean NDVI = 0.657, mean amplitude = 0.786, and mean coefficient of variation = 26.9% (Table 4). HMM state assignments linked in the phenology workflow yielded the same overall state proportions reported in the movement-state analysis: 48.0% travelling-like, 27.7% foraging-like, and 24.2% resting-like. These results indicate that elephant movement states occurred within a strongly seasonal greenness landscape. The repository workflow does not support causal inference that NDVI drove state transitions.

**Table 4.** NDVI phenology summary for the study area.

| Metric | Value |
|---|---|
| Mean NDVI | 0.657 |
| Mean amplitude | 0.786 |
| Mean coefficient of variation (%) | 26.9 |
| Temporal range | 2020-01-01 to 2024-12-18 |
| Pixels sampled in R phenology summary | 100,000 |

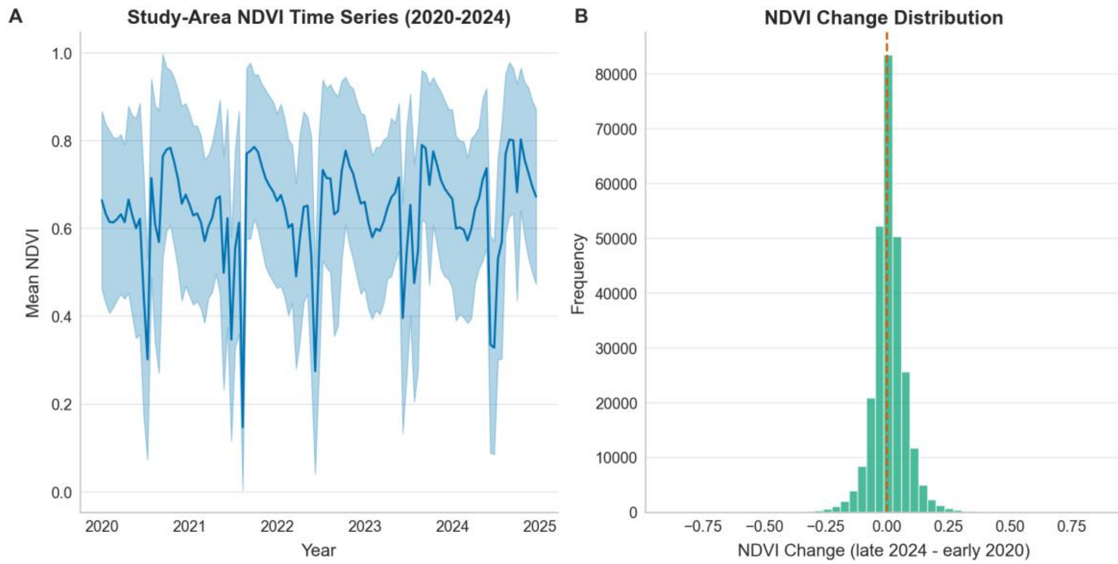


***Figure 3.*** *MODIS NDVI time series for the study area from 2020 to 2024. NDVI is interpreted as vegetation greenness.*

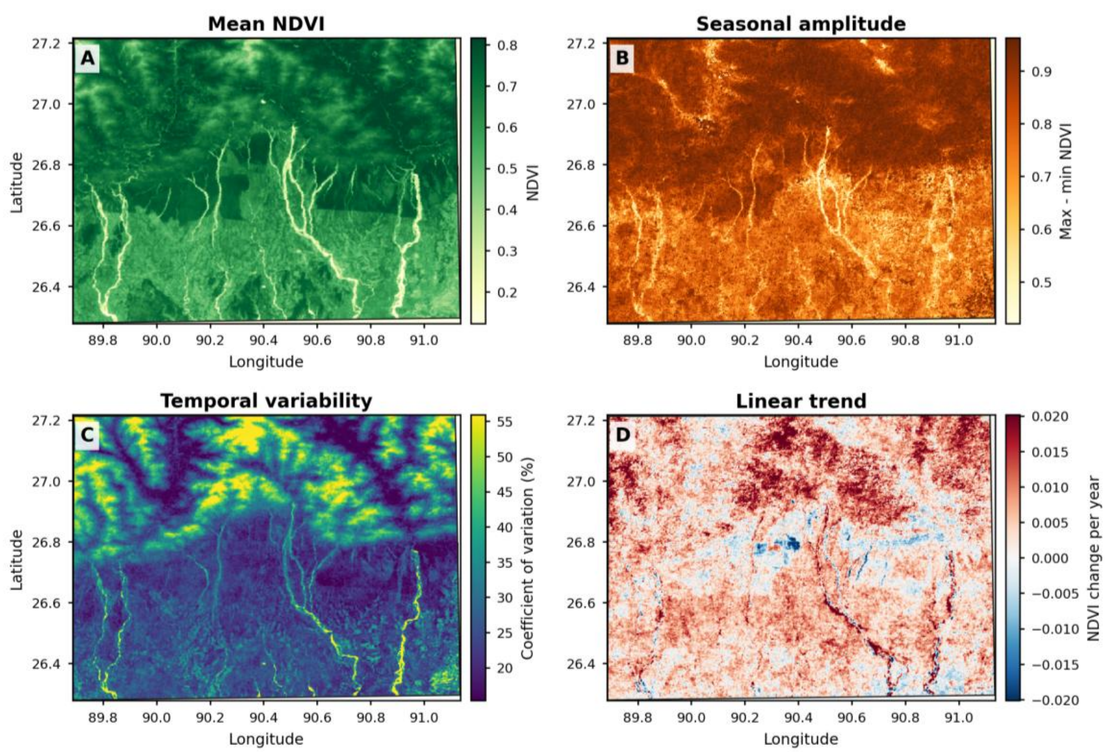


***Figure 4.*** *Spatial summaries of MODIS NDVI phenology across the study area, 2020-2024. Panels show (A) mean NDVI, (B) seasonal amplitude, (C) temporal variability as coefficient of variation, and (D) linear NDVI trend. Mapped values represent vegetation greenness metrics rather than direct forage quality or intake.*

### *Seasonal home-range dynamics*

Seasonal KDE estimates showed larger dry-season than monsoon 95% ranges for all four elephants (Table 5). The strongest seasonal contrast occurred for GMC_04, whose dry-season 95% range was 347.8 km2 compared with 123.7 km2 during the monsoon. GMC_01 and GMC_02 showed modest dry-season expansion, while GMC_03 had the smallest seasonal ranges and fewer fixes.

**Table 5.** Seasonal home-range areas estimated with KDE_href.

| Elephant | Season | n Fixes | 95% Area ($km^2$) | 50% Area ($km^2$) |
|---|---|---|---|---|
| GMC_01 | Monsoon | 4,930 | 689.2 | 107.9 |
| GMC_01 | Dry | 10,018 | 717.6 | 121.9 |
| GMC_02 | Monsoon | 4,853 | 280.4 | 31.4 |
| GMC_02 | Dry | 5,583 | 295.6 | 56.5 |
| GMC_03 | Dry | 1,483 | 71.3 | 9.9 |
| GMC_03 | Monsoon | 749 | 43.1 | 4.9 |
| GMC_04 | Dry | 7,614 | 347.8 | 51.4 |
| GMC_04 | Monsoon | 4,348 | 123.7 | 25.7 |

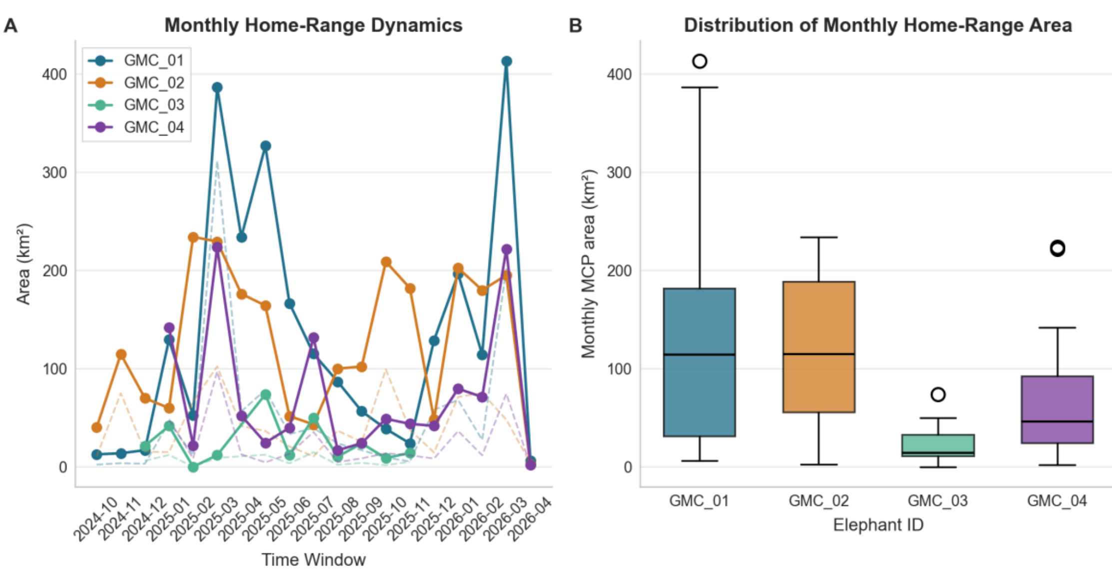


***Figure 5.*** *Seasonal KDE home-range dynamics for collared elephants. Polygons describe seasonal space use from KDE_href estimates.*

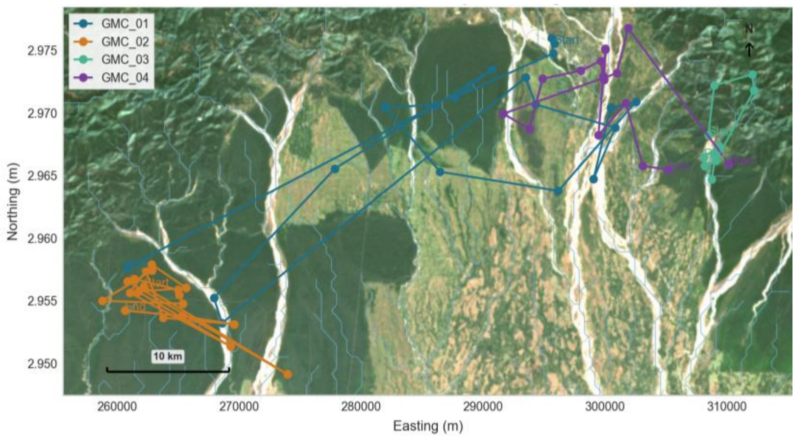


***Figure 6.*** *Seasonal centroid shifts between monsoon and dry-season KDE ranges. Arrows summarize directional shifts in estimated seasonal range centroids.*

### *Seasonal-polygon overlap*

Pairwise seasonal-polygon intersections indicated high shared seasonal space use for GMC_01-GMC_04 and GMC_01-GMC_02 (Table 6). The PHR index exceeded 100 for those pairs because the workflow summed intersections across non-dissolved seasonal polygons. These values therefore identify repeated seasonal intersection, not a bounded percent overlap of a single home range.

**Table 6.** Seasonal-polygon overlap between elephant pairs. PHR is reported as a workflow index based on summed seasonal intersections; UDOI is an approximation from the same polygon areas.

| Pair | Overlap (km2) | Area 1 (km2) | Area 2 (km2) | PHR index | UDOI |
|---|---|---|---|---|---|
| GMC_01 - GMC_04 | 702.2 | 1,406.8 | 471.5 | 148.9 | 0.748 |
| GMC_01 - GMC_02 | 590.7 | 1,406.8 | 575.9 | 102.6 | 0.596 |
| GMC_01 - GMC_03 | 49.7 | 1,406.8 | 114.5 | 43.4 | 0.065 |
| GMC_03 - GMC_04 | 29.6 | 114.5 | 471.5 | 25.8 | 0.101 |

### *Exploratory anomaly screening*

The anomaly workflow identified 3,729 statistical outliers, representing 9.4% of all fixes (Table 7). The isolation forest component flagged 1,979 fixes under contamination = 0.05. Rolling movement summaries identified 848 behavioural-shift flags, and immobility screening identified 12,117 immobile fixes. These categories are screening outputs and are not mutually interpreted as confirmed ecological events.

**Table 7.** Exploratory anomaly-screening outputs from the repository workflow.

| Screening component | Value |
|---|---|
| Records screened | 39,578 |
| Statistical outliers | 3,729 |
| Statistical outlier rate | 9.42% |
| Isolation forest flags | 1,979 |
| Isolation forest contamination | 0.05 |

| Screening component | Value |
|---|---|
| Isolation forest estimators | 200 |
| Rolling behavioural-shift flags | 848 |
| Immobility flags | 12,117 |

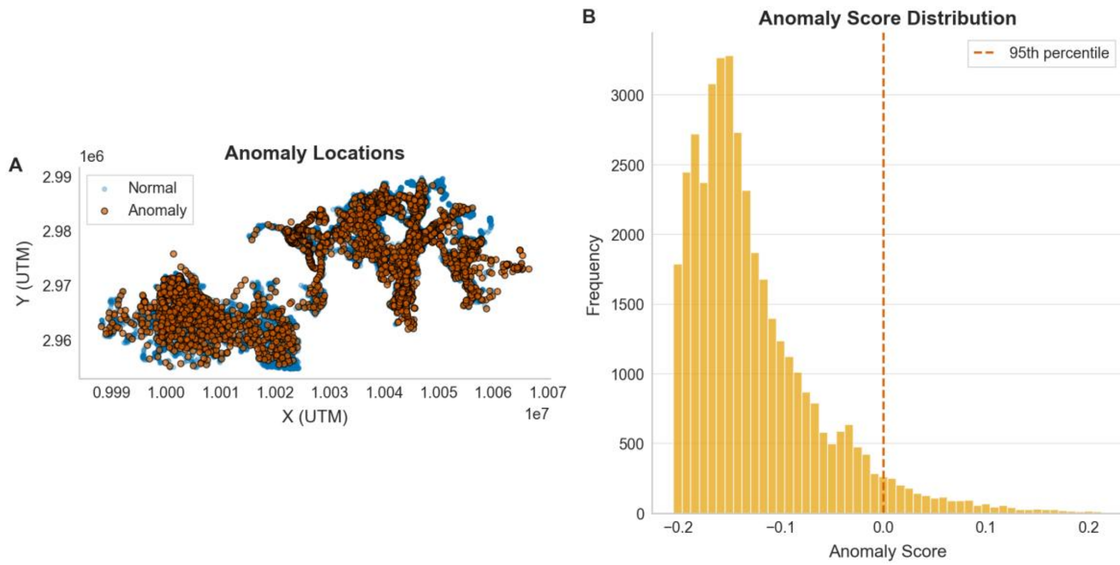


***Figure 7.*** *Spatial distribution of GPS fixes flagged by the anomaly-screening workflow. Points identify candidate records for validation rather than confirmed disturbance or displacement events.*

## Discussion

### *Movement-state allocation and behavioural dynamics*

Movement-state modelling indicates that travelling-like movement dominated the telemetry record, although substantial inter-individual variation was evident. This heterogeneity suggests that movement strategies are not uniform across individuals, but instead reflect context-dependent behavioural responses to environmental and landscape conditions. The high prevalence of travelling-like states, particularly in *GMC_02*, indicates sustained directional movement consistent with large-scale space use in a heterogeneous region system.

The transition dynamics provide stronger mechanistic insight than state proportions alone. Elevated self-transition probabilities for travelling-like movement indicate behavioural persistence once directional movement is initiated, implying that elephants commit to displacement over extended sequences. In contrast, resting-like and foraging-like states exhibited lower persistence and higher transition frequencies, consistent with localized and short-duration behavioural modes. This pattern aligns with expectations from movement ecology theory, where animals alternate between intensive local search and extensive displacement phases within heterogeneous environments. However, because states were inferred using *momentuHMM* from movement metrics, they represent statistical constructs rather than directly observed behaviours. Consequently, interpretation as activity budgets remains provisional and requires independent behavioural validation.

### *Scale-dependent search behaviour and ARS interpretation*

First-passage time (FPT) analysis revealed kilometre-scale movement clustering, with the strongest signal observed in *GMC_03*. These clustering patterns are consistent with area-restricted search behaviour, where animals concentrate movement within resource-rich or otherwise important areas.

A critical limitation is the upper-bound constraint of the radius search (5,000 m). For three individuals, the variance peak occurred at this boundary, indicating that the true scale of clustering likely exceeds the tested range. As a result, reported ARS scales should be interpreted as **lower-bound estimates** rather than definitive ecological scales. This constraint materially affects inference and prevents precise identification of patch size or search radius.

Despite this limitation, the identification of seven candidate ARS zones provides a robust spatial hypothesis for field validation. These zones likely represent areas of ecological or anthropogenic importance, including concentrated forage, water sources, crop fields, or constrained movement pathways. Without independent validation data, ARS signals remain movement patterns and should not be directly equated with foraging behaviour.

### *Environmental seasonality and movement responses*

Seasonal analyses indicate consistent expansion of dry-season home ranges across all individuals, with particularly pronounced expansion in *GMC_04*. This pattern is consistent with theoretical expectations that herbivores increase ranging behaviour under conditions of resource dispersion. In seasonal environments, reduced water availability and declining vegetation productivity can necessitate broader spatial exploration to meet energetic requirements.

This interpretation is supported by previous findings that elephant movement tracks precipitation-driven vegetation dynamics, as demonstrated by Bohrer et al., and that landscape configuration influences ranging behaviour in human-modified systems (Chan et al.). However, the present analysis does not explicitly model environmental drivers of movement, and therefore cannot isolate causal mechanisms. NDVI phenology indicates strong seasonal greenness variability, but its role remains contextual rather than explanatory in the current framework. Because NDVI represents vegetation greenness rather than forage quality or intake, its ecological interpretation is inherently limited. The absence of formal movement–environment modelling means that associations between greenness and behaviour remain inferred rather than statistically demonstrated.

Centroid shifts further indicate that seasonal dynamics involve not only expansion of space use but also relocation of activity centres. From a management perspective, this suggests that elephants actively reconfigure spatial use across seasons rather than simply expanding within fixed ranges.

### *Seasonal overlap and spatial interaction*

Pairwise overlap analyses identified repeated seasonal spatial intersection among specific individuals, particularly *GMC_01–GMC_04 and GMC_01–GMC_02*. These patterns suggest shared use of key landscape features, potentially including movement regions, resource hotspots, or constrained pathways.

However, the overlap metric used (PHR index) is not directly interpretable as a bounded percentage because it aggregates intersections across non-dissolved seasonal polygons. Consequently, values exceeding 100% do not indicate complete overlap but rather repeated spatial intersection across temporal partitions. The UDOI metric provides a complementary index, but both measures remain sensitive to methodological choices, including bandwidth selection and seasonal segmentation. Therefore, overlap results should be interpreted comparatively rather than absolutely, emphasizing relative spatial interaction rather than precise quantification of shared space.

***Anomaly detection and ecological interpretation***

Anomaly screening identified multiple classes of unusual movement patterns, including statistical outliers, isolation-forest detections, behavioural shifts, and immobility events. These outputs provide a useful prioritization framework for identifying candidate events or locations of interest.

However, the absence of independent validation data represents a critical limitation. Without corroborating information—such as conflict records, habitat features, or collar diagnostics—these anomalies cannot be attributed to ecological processes such as disturbance, displacement, or resource exploitation. Instead, they should be interpreted as **screening indicators** that guide further investigation. The strongest application of anomaly detection lies in integrating these flags with external datasets, including human activity, infrastructure, and seasonal resource availability.

***Conservation implications***

The integration of movement states, clustering, seasonal dynamics, overlap patterns, and anomaly screening identifies candidate monitoring and intervention areas within a fragmented region system. These include:

- ARS zones (potential resource concentration or conflict areas)
- Dry-season expansion zones (increased ranging pressure)
- Seasonal centroid shifts (dynamic habitat use)
- High-overlap areas (shared movement regions)
- Anomaly clusters (potential disturbance or conflict signals)

Importantly, these outputs do not define management units but rather prioritize locations for field validation and monitoring. Given the small sample size (n = 4), conservation inference must remain individual-specific and should not be generalized to the broader population without additional data.

***Sensitivity and uncertainty***

*Several methodological and data limitations constrain inference:*

- *HMM-derived states are probabilistic and require behavioural validation*
- *FPT results are truncated by the radius ceiling (5,000 m)*
- *NDVI captures greenness but not forage quality or intake*
- *Seasonal KDE estimates are descriptive and sensitive to bandwidth selection*
- *Overlap metrics are workflow-dependent and not strictly bounded*
- *Anomaly detection lacks independent validation*

These limitations collectively restrict interpretation to pattern identification rather than causal inference.

### *Conclusions*

This study provides a multi-method assessment of elephant movement ecology in a fragmented Himalayan foothill region, integrating movement-state modelling, spatial clustering, environmental context, and seasonal space-use analysis. The results demonstrate pronounced individual variation in movement strategies, *kilometre-scale* clustering consistent with area-restricted search, and systematic expansion of home ranges during the dry season.

The dominant pattern of travelling-like movement suggests that elephants frequently engage in sustained displacement across heterogeneous landscapes, while localized clustering highlights areas of potential ecological or anthropogenic importance. Seasonal expansion and centroid shifts indicate dynamic spatial responses to environmental variability, particularly under resource-limited conditions.

However, all interpretations are necessarily conservative. Movement states are inferred proxies, clustering scales are lower-bound estimates, *NDVI* is an indirect environmental indicator, home ranges are descriptive summaries, overlap metrics are comparative indices, and anomaly outputs are screening tools. Within these constraints, the study provides a reproducible framework for identifying priority areas for monitoring and validation.

Future work should focus on integrating environmental covariates directly into movement models, expanding sample size, and incorporating independent field validation to establish causal links between environmental drivers and movement *behaviour*. Such advances are essential for translating movement ecology insights into effective conservation strategies in human-dominated landscapes.

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**Data availability:** GPS telemetry data used in this study are held by the Department of Forests and Park Services, Royal Government of Bhutan, and are not publicly available due to institutional data-sharing restrictions and the sensitive nature of wildlife tracking data. Access may be granted upon reasonable request, subject to approval by the relevant authorities.

All analysis scripts, processing workflows, and supporting outputs are maintained within the project repository. The analyses presented in this manuscript are based on reproducible workflows implemented in R and Python. Relevant materials required to reproduce the results, including scripts and processing summaries, may be made available by the corresponding author upon reasonable request.

**Conflict of interest.** No conflict-of-interest statement was available in repository metadata.

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