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Method Article

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Segmentation and profile-based classification of movement strategies from animal tracking data

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Abstract

Background

Classifying animal movement strategies from GPS tracking data is essential for understanding space use, population dynamics and conservation planning. However, existing approaches either require strong parametric assumptions of the functional form, large labelled datasets (i.e., expert-annotated) for machine learning, or do not provide ways to quantify uncertainties of the classification. These limitations create barriers for researchers working with novel species or small sample sizes.

Methods

We present a profile-based classification framework consisting of three steps. First, trajectories are segmented using breakpoint detection applied to Net Squared Displacement (NSD) time series. Next, movement metrics are extracted from each segment and classified by comparing them to empirically derived behavioural profiles via Z-score distances transformed to softmax probabilities. Finally, uncertainty of the classified movement strategies is obtained by bootstrapping, and each assignment receives a credibility rating based on the overlap of bootstrap confidence intervals between the strategies. We validated our proposed framework through simulations and applied it to GPS tracking data from two ecologically contrasting species: gray wolves (*Canis lupus*; 44 individuals) and northern lapwing (*Vanellus vanellus*; 15 individuals).

Results

Simulations showed that 5–10 training segments per movement strategy are enough for reliable classification, with an overall accuracy of 91.1% across residential, floating, and dispersal strategies. A segment duration of 30–60 days was required for confident discrimination of residential and floating behaviour. For wolves, 83% of classified segments received High or Medium credibility, with residency, floating and dispersal phases distinguished. For lapwings, migration segments were identified with high credibility (96%), while residency–floating discrimination was more challenging, but expected and confirmed by domain experts.

Conclusions

The profile-based framework provides an accessible, interpretable alternative to fitting parametric functions to NSD time series and machine learning approaches. Our framework requires a modest training data set and results in probabilistic classifications with uncertainty estimates. An R package (*moveprofile*) implementing the complete workflow is available on GitHub. The framework is applicable to any tracked species where distinct movement strategies can be identified from expert knowledge.

Keywords: movement ecology, movement strategy identification, Net Squared Displacement, moveprofile, profile-based classification, telemetry, trajectory segmentation, gray wolf, northern lapwing

Background

Animal movement is one of the most fundamental processes in ecology, with far-reaching consequences for individual fitness, population dynamics, and ecosystem functioning [1,2]. The way in which animals move through their environment reflects underlying movement strategies that are shaped by the interplay between their internal state, their navigation capacity, and external factors such as resource distribution, predation risk, and reproductive opportunities [2,3]. Among vertebrates, these strategies span a remarkable spectrum, from localised residency within stable home ranges to long-distance migration between seasonal habitats, exploratory nomadism searching for ephemeral resources, and natal dispersal that maintains genetic connectivity among populations [4,5]. These distinct movement strategies are not merely descriptive patterns, but represent induced responses to ecological pressure that directly influence survival, reproduction, or population persistence [6,7]. Understanding and identifying movement strategies of individual animals has become increasingly important for conservation planning [8], predicting disease transmission dynamics [9], managing human-wildlife conflict [10], and forecasting species responses to environmental change [11].

Despite the ecological importance of movement strategies, quantifying them from tracking data remains methodologically challenging, as existing approaches each carry distinct assumptions and limitations [4,12,13]. A commonly used approach fits different parametric models to observed Net Squared Displacement (NSD) of trajectories, each representing a distinct movement strategy [4,14]. While NSD has a direct mechanistic interpretation, this framework makes strong assumptions about trajectory functional shapes and provides limited guidance when observed patterns deviate from commonly used functional forms [15]. Alternatively, clustering approaches offer data-driven alternatives by grouping similar movement metrics without parametric assumptions, yet they struggle with arbitrary cluster number selection and provide hard (categorical) classifications assigning each segment to a single class without probabilistic assessments of uncertainty [12]. Machine learning methods, including random forests and neural networks, have demonstrated high classification accuracy when trained on large, balanced datasets [16], yet they are typically less interpretable, making it harder to attribute classifications to specific movement characteristics, and their data requirements often exceed what is available for rare species or behaviours [17]. Critically, most existing approaches lack formal frameworks for quantifying classification uncertainty arising from limited training data, leaving practitioners without quality indicators to assess when classifications are reliable versus when additional data collection or expert validation is warranted. What is missing is an approach that combines modest training-data requirements, transparent and ecologically interpretable

decisions, and an explicit measure of classification confidence. We address this gap here.

Here, we present a profile-based classification framework that segments trajectories into different segments and classifies these segments to different movement strategies with classification uncertainty. The method constructs reference behavioural profiles from expert-labelled training segments (sections of trajectories with known movement strategy), capturing characteristic patterns in NSD across time. Classification proceeds by comparing new segments to these profiles, yielding not only strategy assignments but also confidence metrics derived through bootstrap resampling. This quantifies uncertainty arising from limited training data and reflects it in the reported classification probabilities [18,19].

Our primary objectives here are threefold. First, we develop and validate the methodology with simulated data with known truth, then we apply it to two species with contrasting movement ecologies: a mammal (gray wolf; *Canis lupus*) and a bird (northern lapwing; *Vanellus vanellus*). Second, we implement bootstrap uncertainty quantification to distinguish high-confidence classifications from ambiguous cases that require expert review or additional data collection. Third, we provide practical guidance on implementation decisions, including training data requirements, selection of movement metrics, and the temporal resolution of analysis. To make the framework readily accessible in practice, we implement the complete workflow, from trajectory segmentation through profile-based classification and bootstrapping uncertainties in the open-source R package *moveprofile*.

Methods

The overall approach comprises several sequential steps (Fig. 1). We first aggregate GPS positions into time windows of several hours and derive a time series of NSD (*Data preprocessing and NSD calculation; Fig. 1*). We then search for breakpoints to partition the trajectories into segments (*Trajectory segmentation; Fig. 1*) and extract movement metrics from each segment (*Movement metrics; Fig. 1*). Using expert-labelled training segments, we establish reference profiles for each behavioural class (*Training data and profile construction*) and finally classify unknown segments using softmax-transformed Z-score distances, quantifying uncertainty by bootstrapping over segments (*Classification and uncertainty quantification*). The complete workflow is implemented in the *moveprofile* package, with a reproducible worked example provided as a package vignette.

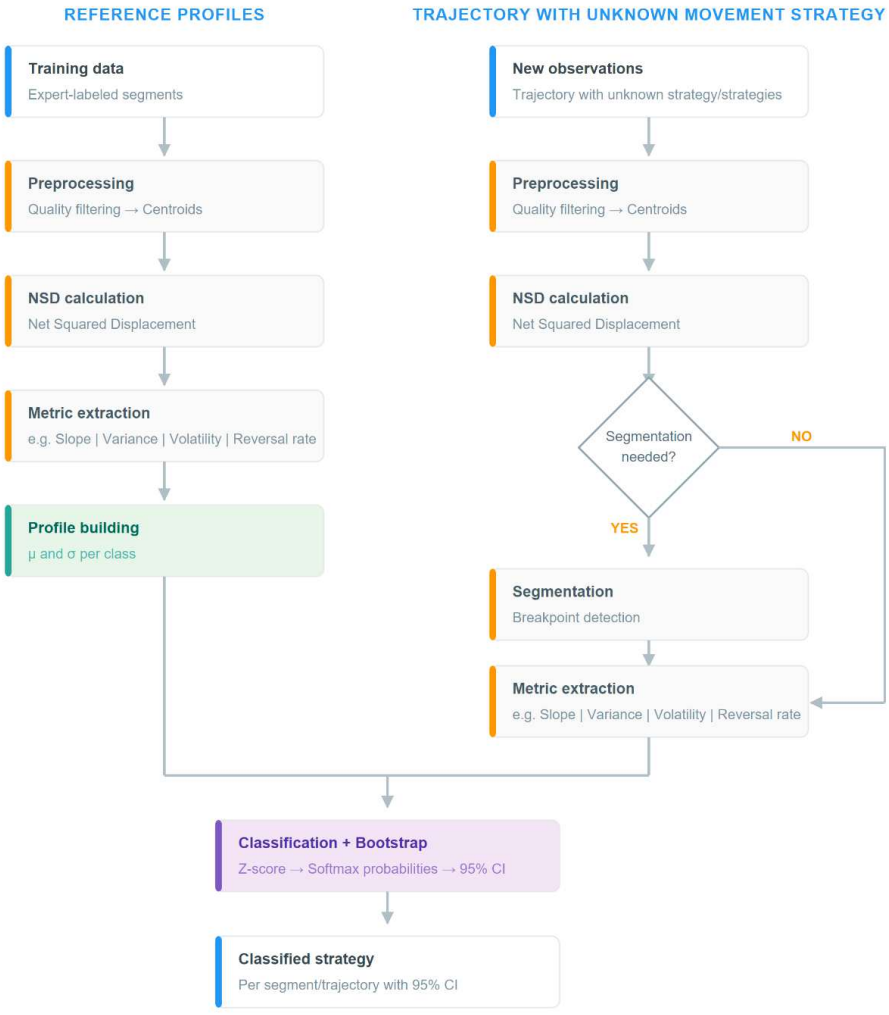


Figure 1. Workflow of the profile-based movement classification framework. Training data (left path) and test data (right path) undergo preprocessing, NSD calculation, and metric extraction. Training segments build reference profiles (mean and standard

deviation per behavioural class), which are used to classify test segments via Z-score distances converted to softmax probabilities. Bootstrap resampling quantifies classification uncertainty, yielding probability estimates with 95% confidence intervals.

Data preprocessing and NSD calculation

We designed the method to work with GPS telemetry data from a tracked animal. We apply quality filters to keep only high-precision locations (e.g., dilution of precision ≤6). To reduce noise from fine-scale movements, we aggregate raw positions into temporal centroids. For a given time interval *Δt*, we calculate the mean position of all GPS fixes within that interval:

$$\bar{x}_{\Delta t} = \frac{1}{n}\sum_{i=1}^{n} x_i\,, \quad \bar{y}_{\Delta t} = \frac{1}{n}\sum_{i=1}^{n} y_i$$

where *n* is the number of observations within the interval. This approach supports multiple temporal resolutions (e.g., 3h, 6h, 12h, 24h, ...), allowing users to choose the appropriate temporal scale for the desired movement strategy detection. Shorter temporal intervals capture fine-scale behavioural transitions, whereas longer intervals suppress daily variation and highlight long-term displacement patterns. The optimal temporal resolution depends on the biology of the studied species and on the intended research question. We recommend using daily-based centroids, but in some cases, this may be too rough (see case studies).

From the centroid time series, we calculate Net Squared Displacement (NSD), a widely used metric in movement ecology that quantifies the squared Euclidean distance between an animal's current position and its starting location [4]. For a position at time *t*, we define NSD as:

$$NSD_{2D}(t) = (x_t - x_0)^2 + (y_t - y_0)^2$$

where (x_0, y_0) represents the initial position and (x_t, y_t) is the position at time *t*. NSD provides a cumulative measure of spatial displacement over time, making it sensitive to changes in movement behaviour. Unlike instantaneous metrics such as step length or turning angle, NSD integrates movement history, allowing for the detection of long-term behavioural patterns.

For species that exhibit significant vertical displacement (e.g., altitudinal migrants, marine divers), NSD can be extended to three dimensions where *z* represents altitude or depth:

$$NSD_{3D}(t) = (x_t - x_0)^2 + (y_t - y_0)^2 + (z_t - z_0)^2$$

Trajectory segmentation

Movement strategies are not static; animals transition between them in response to ecological cues. To identify these transitions objectively, we apply a grid-search breakpoint detection algorithm to the NSD time series. For this purpose, we evaluate all

possible breakpoint combinations within user-defined temporal ranges. For each candidate breakpoint combination, we fit and assess a piecewise linear model using Akaike Information Criterion (AIC), which balances model complexity against goodness-of-fit. We select the breakpoint configuration with the lowest AIC as optimal segmentation. This approach partitions the trajectory into discrete segments, each representing a distinct movement strategy.

Within each segment *j* (a contiguous section of the NSD time series between two consecutive breakpoints), we model NSD as:

$$NSD_j(t) = \alpha_j + \beta_j \cdot t + \epsilon_j$$

where α_j is the intercept, β_j is the regression slope, representing the rate of change in squared displacement per unit time, and ε_j represents residual error. The slope has a direct ecological meaning: values near zero indicate residency, while positive or negative values suggest migration or exploration, respectively.

We use three criteria that control segmentation: 1) minimum gap between breakpoints (default threshold: 5 days), 2) minimum segment size (default: 5 observations), and 3) search step size (default: 3 days). Users should adjust these values based on species ecology and GPS sampling frequency. Note that uncertainty arising from segmentation parameter selection is not propagated through bootstrap resampling and represents an additional source of uncertainty in the final classifications.

Training data and profile construction

Classification requires a training dataset of expert-labelled segments from tracked individuals. A species expert should perform this classification, based on visual inspection of trajectories. The number and definition of movement strategies depend on the study species; for example, wolves may exhibit residency (territorial), floating (nomadic), and dispersal behaviours, while migratory birds show residency, some form of nomadism or floating, and migration.

For each training segment, we calculate the movement metrics described in the next section, yielding a training matrix **X** ∈ ℝ^(n×p), where *n* is the total number of training segments across all behavioural classes and *p* is the number of metrics. Each row of the matrix represents one segment, and each column represents a metric value:

$$[\mathbf{X} \mid \mathbf{y}] = \begin{pmatrix} x_{1,1} & x_{1,2} & \cdots & x_{1,p} & c_1 \\ x_{2,1} & x_{2,2} & \cdots & x_{2,p} & c_2 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ x_{n,1} & x_{n,2} & \cdots & x_{n,p} & c_C \end{pmatrix}$$

where the last column represents the label vector **y**, with c i ∈ {1, ..., C} denoting the behavioural class of segment *i*. From this matrix, class-specific mean vectors **μ**_*c* and standard deviation vectors **σ**_*c* are computed separately for each behavioural class *c*:

$$\boldsymbol{\mu}_c = \frac{1}{n_c}\sum_{i \in c} \mathbf{x}_i\,, \quad \boldsymbol{\sigma}_c = \sqrt{\frac{1}{n_c - 1}\sum_{i \in c} (\mathbf{x}_i - \boldsymbol{\mu}_c)^2}$$

where n_c is the number of training segments belonging to class c. These vectors define the characteristic "profile" of each behavioural class in metric space and serve as reference profiles for classifying unknown segments.

Training data should ideally span multiple individuals and, where possible, different temporal periods to capture natural variability within each behavioural class and to avoid overfitting to individual-specific movement patterns.

Movement metrics

From each segment, movement metrics quantify behavioural signatures. The framework allows flexibility in metric selection; users should choose metrics distinguishing between relevant movement strategies based on the ecology of the studied species.

The framework currently provides six metrics (slope, R^2, rolling variance, volatility, reversal rate, and autocorrelation), all of which we evaluated in our simulations. The slope can be used in either signed or absolute form, the latter where a strategy involves displacement in both directions (see the lapwing case study). We recommend the following four core metrics that collectively provide the best discriminatory performance:

Slope (β) of NSD quantifies the rate of spatial displacement, derived from linear regression of NSD on time *t*:

$$\beta = \frac{\sum_{i=1}^{n}(t_i - \bar{t})\left(NSD_i - \overline{NSD}\right)}{\sum_{i=1}^{n}(t_i - \bar{t})^2}$$

Steeply positive slopes indicate rapid, directional movement away from the origin, characteristic of dispersal or outward migration, while negative slopes may reflect a return phase or inward migration, and slopes near zero suggest residency.

Rolling variance captures local variability in NSD over a sliding window of width *w*:

$$\text{RollingVar} = \frac{1}{n - w + 1}\sum_{i=1}^{n-w+1} \text{Var}\left(NSD_{i:i+w-1}\right)$$

High rolling variance indicates unstable or exploratory movement patterns, while low values suggest consistent behaviour within the segment.

Volatility measures short-term movement consistency as the mean absolute change between consecutive NSD values:

$$\text{Volatility} = \frac{1}{n-1}\sum_{i=1}^{n-1}|NSD_{i+1} - NSD_i|$$

High volatility characterises erratic, fluctuating displacement typical for floating behaviour, while low volatility indicates smooth, gradual changes in displacement characteristic of animals remaining within a confined area. Unlike rolling variance, which reflects variability over a local time window, volatility captures roughness in movement at the level of consecutive steps, providing complementary information at a finer temporal scale.

Reversal rate quantifies oscillatory behaviour by measuring the proportion of directional changes in the NSD series:

$$\text{ReversalRate} = \frac{1}{n-2}\sum_{i=1}^{n-2}\mathbb{1}\left(\text{sign}(\Delta_i) \neq \text{sign}(\Delta_{i+1})\right)$$

where $\Delta_i = NSD_{i+1} - NSD_i$. High reversal rates indicate back-and-forth movement without net displacement, while low rates characterise unidirectional movement.

These four metrics collectively capture directionality (slope), local stability (rolling variance), short-term consistency (volatility), and oscillatory patterns (reversal rate), providing effective discrimination across residency, migration, and exploratory strategies in our case studies.

Beyond the four core metrics, the framework includes additional optional metrics that may improve classification in specific ecological contexts. $\mathbf{R^2}$ of the slope regression quantifies the proportion of variance in NSD explained by the linear trend; high values indicate movement that follows a consistent directional trajectory, while low values reflect irregular or oscillatory patterns. **Autocorrelation** quantifies directional persistence as the lag-1 autocorrelation of the NSD time series, measuring the correlation between NSD(t) and NSD(t−1); high values indicate persistent directional movement characteristic for dispersal, while low values reflect erratic or oscillatory displacement typical for floating or residential behaviour. Researchers may also implement custom metrics tailored to their study system. When provided, they can show a clear separation between the behavioural classes of interest and carry an interpretable ecological meaning.

Classification and uncertainty quantification

To classify an unknown segment, we use a distance-based approach in which standardised Z-scores quantify how much the unknown segment deviates from each reference profile. For an unknown segment with a metric vector $\mathbf{x}_{\text{unknown}}$, we calculate standardised distances (Z-scores) to each behavioural class *c*:

$$Z_{c,j} = \frac{x_{\text{unknown},j} - \mu_{c,j}}{\sigma_{c,j}}$$

where j indexes movement metrics and c indexes behavioural classes. The overall distance to class c is the mean absolute Z-score:

$$D_c = \frac{1}{p}\sum_{j=1}^{p} |Z_{c,j}|$$

This metric quantifies, in standard deviations, how far the test segment lies from the typical profile for each behavioural class. Smaller distances indicate greater similarity to the class.

To convert distances into interpretable class membership probabilities, we apply the softmax transformation:

$$P(c|\mathbf{x}_{\text{test}}) = \frac{\exp(-D_c/T)}{\sum_{c'=1}^{C}\exp(-D_{c'}/T)}$$

where C is the number of classes, and T is a temperature parameter (set to T = 1 by default). The softmax function converts raw distances into class membership probabilities, assigning higher probabilities to closer profile matches while ensuring all probabilities sum to unity. The temperature parameter T controls classification sharpness: at low values, the highest-probability class dominates (approaching a hard assignment), while higher values produce more uniform distributions. At T = 1 (default), probabilities directly reflect relative distances without additional sharpening; a segment equidistant between two strategies receives similar probabilities for both, transparently flagging ambiguous cases.

To quantify classification uncertainty, we implement bootstrap resampling after segmentation of the identified segments (see Trajectory segmentation). Bootstrap resampling, therefore, does not propagate uncertainty arising from breakpoint detection or segmentation parameter selection, which represents additional sources of uncertainty acknowledged in the Limitations section. Profile parameters are estimated from *B_profile* resamples (default: 100) of the training data, each sample of the same size as the original training set and drawn with replacement, independently within each behavioural class. For each resample, class parameters (μ_c, σ_c) are recalculated and classification probabilities recomputed, capturing uncertainty from finite training sample sizes only. Double bootstrap (nested resampling of both profile-building and unknown-segment data) additionally resamples observations within the unknown segment *B_unknown* times (default: 100), yielding *B_unknown* × *B_profile* = 10,000 iterations that propagate variability from both training and unknown-segment data. Resampling of training data is performed within each behavioural class independently of individual identity; multiple segments from the same individual are treated as separate observations. We report results as mean probability with 95% confidence intervals, for example: Residency: 78.2% [62.1%, 91.3%].

Classification reliability is then rated automatically from the relationship between confidence intervals across strategies and reported as a *credibility* score alongside each assignment. A segment is rated High when the confidence interval of the assigned class does not overlap the interval of any alternative strategy, indicating unambiguous classification. It is rated Medium when intervals overlap but no class mean falls within another class's interval; such classifications remain reliable, although the separation between strategies is less distinct. It is rated Low when the interval of the assigned class contains the mean probability of one alternative strategy (or vice versa), and Unclear when two or more alternatives meet this condition. Low and Unclear segments should be treated with caution and verified by expert review, and the framework allows users to override the automatic assignment for such cases.

Simulation design

To evaluate framework performance under controlled conditions with known ground truth, we simulated trajectories representing three movement strategies with characteristic NSD dynamics (Fig. 2). We simulated residential trajectories with low baseline NSD values and multi-frequency oscillations representing daily and weekly activity patterns, with occasional short-duration excursions that return to a central location. We simulated floating trajectories using a random walk process with variable step sizes, frequent directional reversals, and occasional large displacements, but without persistent directional movement. We built dispersal trajectories around a strong positive linear trend with superimposed stopovers creating temporary plateaus and autocorrelated noise reflecting movement persistence. Each trajectory type incorporated observation noise calibrated to produce realistic metric distributions comparable to empirical tracking data.

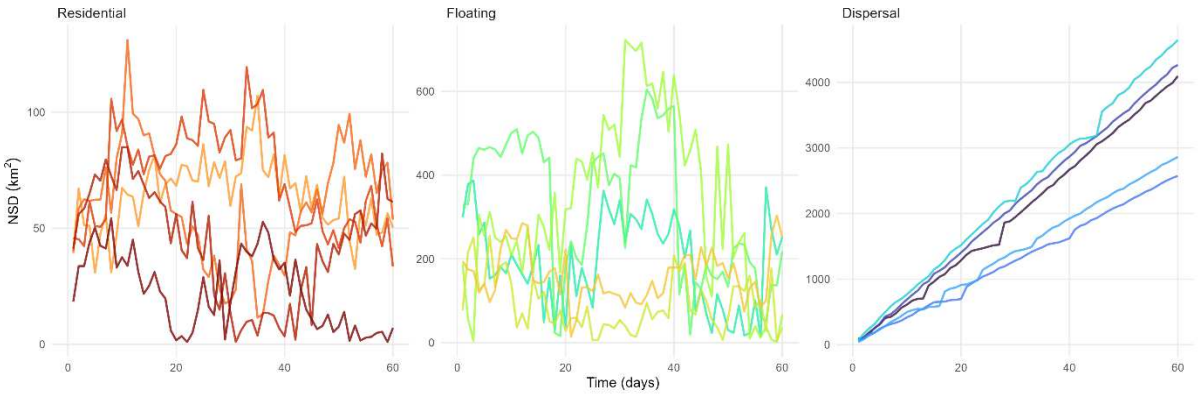


Figure 2. Simulated Net Squared Displacement (NSD) trajectories for three movement strategies. Residential trajectories (a) show low-amplitude oscillations with occasional excursions returning to a central location. Floating trajectories (b) display erratic, high-variance displacement without directional persistence. Dispersal trajectories (c) exhibit strong positive trends with occasional stopovers. Five replicates shown per strategy; note different y-axis scales.

Empirical data

We applied the classification framework to GPS tracking data of two species (gray wolf and northern lapwing) with contrasting movement ecologies.

Gray wolves: GPS telemetry data were obtained from wolves monitored across Central Europe (Czechia, Germany, Austria, and Poland) between 2016 and 2025. The dataset comprised 44 individuals: 13 used for training with expert-assigned behavioural classifications (23 segments total), and 31 for classification. Training and test datasets contained no overlapping individuals. Collars recorded locations at variable intervals (from 1 to 12 hours); positions were aggregated into daily (24-hour) centroids (Additional file 1: Table S1, Table S2).

Northern lapwings: GPS tracking data were collected from 15 lapwings breeding in Czechia and migrating to wintering grounds in Spain and France between 2024 and 2026. Four individuals (46 segments) with expert-assigned classifications served as training data; 11 individuals were classified. Positions were aggregated into 12-hour centroids to capture faster behavioural transitions (Additional file 1: Table S3, Table S4).

Software and use of large language models

All analyses were carried out in R version 4.4.1 [20]. The workflow is implemented in the *moveprofile* package, with a reproducible worked example provided as a package vignette.

During the preparation of this manuscript, the authors used Anthropic's Claude (a large language model) for language editing, grammar checking, and text refinement. All AI-assisted suggestions were critically reviewed, edited where necessary, and approved by the authors. The tool was not used for data analysis, scientific interpretation, or the generation of results. The authors take full responsibility for the integrity, accuracy, and originality of all content.

Results

We evaluated the profile-based classification framework through simulation validation followed by empirical application to two species. First, we assessed classification performance using simulated trajectories with known ground truth to establish baseline accuracy and examine the effects of training sample size, segment duration, and metric selection. We then applied the framework to GPS tracking data from gray wolves and northern lapwings, representing contrasting movement ecologies at fundamentally different spatial and temporal scales.

Simulation Validation

Classification accuracy increased steeply with training sample size (Fig. 3a). With only two segments per class, it was low and strategy-dependent, but by five segments dispersal and floating approached 90% probability and residential ~75%, and by ten all three exceeded 85%. Beyond ten segments, gains were marginal, indicating that 5–10 segments per class suffice when behavioural classes are well-defined.

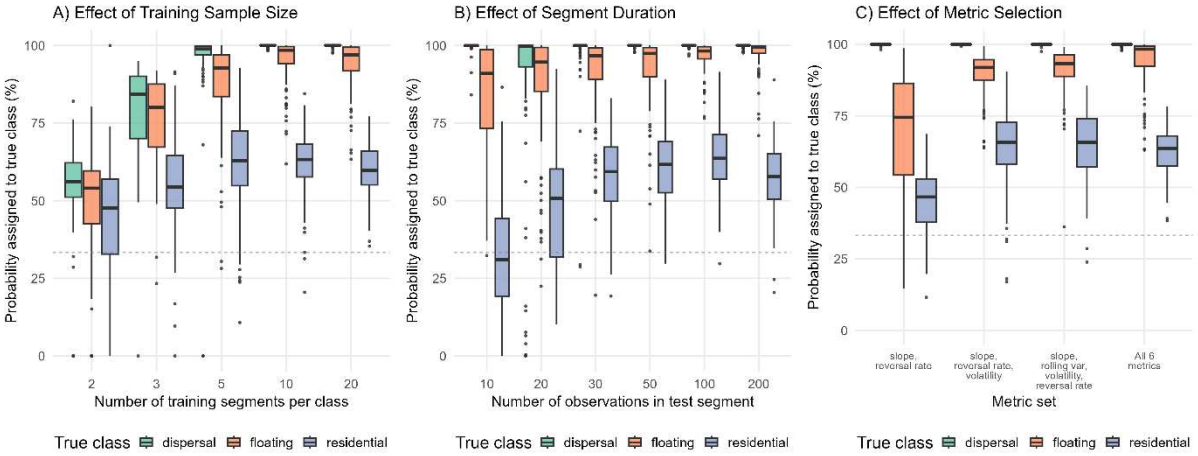


Figure 3. Effects of training sample size, segment duration, and metric selection on classification accuracy. Panels show the effect of (a) training sample size, (b) segment duration, and (c) metric selection. The dashed line indicates chance performance (33%). In (a), test segments contained 60 observations; in (b), 10 training segments per class were used; in (c), 10 training segments and 60-observation test segments. Boxplots show median and interquartile range across 100 replicates.

Segment duration showed a similar pattern (Fig. 3b). Dispersal was reliably identified even from short 10-observation segments, whereas residential probability rose from 25–40% at 10 observations to 70–85% at 50 and reached a ceiling at ~100. Residential and floating thus need substantially longer series than dispersal, because their discrimination relies on accumulating the oscillatory return-and-reversal signal that distinguishes them.

Metric selection mattered for the same reason (Fig. 3c). Slope and reversal rate alone classified dispersal well (median >95%) but left residential near chance (~45%); adding volatility raised residential to ~65%, and the recommended four-metric set (slope, rolling variance, volatility, reversal rate) performed as well as the full six. Which metrics are needed, therefore, depends on the strategies being separated: slope suffices for dispersal, but residential–floating discrimination requires variance-based metrics.

The confusion matrix aggregated across all training sizes showed asymmetric errors (Fig. 4). Overall accuracy was 91.1% (1,636 of 1,796 trials). Floating was classified most accurately (97.5%) and residential least accurately (82.1%), with the dominant error

being one-directional: residential was misclassified as floating in 17.7% of trials, versus only 2.5% in the reverse. Residential and dispersal were almost never confused, reflecting their distinct NSD dynamics (oscillatory versus monotonically increasing); the mechanism behind this asymmetry is taken up in the Discussion.

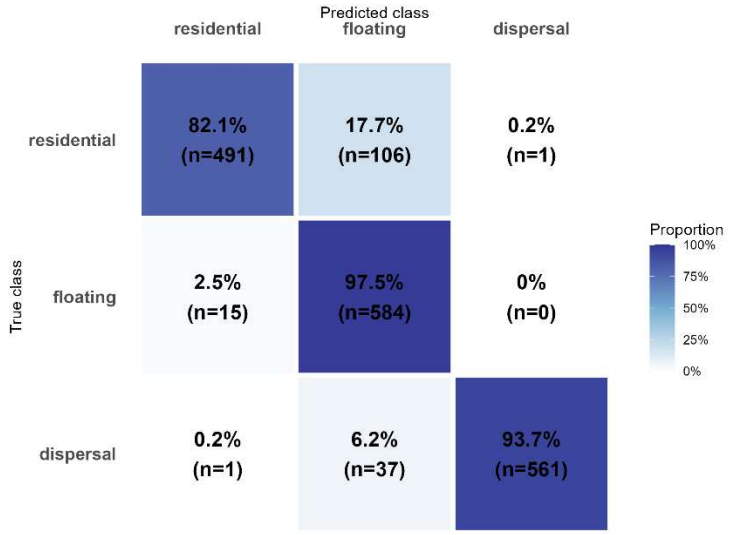


Figure 4. Confusion matrix for simulated trajectory classification. Values show the percentage (count) of segments from each true class (rows) assigned to predicted classes (columns), aggregated across all training sizes (n = 1,796 trials). Overall accuracy was 91.1%, with highest per-class accuracy for floating (97.5%) and lowest for residential (82.1%).

Gray wolf

Study species and movement strategies

Wolves exhibit three movement strategies with important implications for population dynamics, territory establishment, and management [21]. Territorial residents maintain stable home ranges within pack territories, typically characterised by low net displacement from a central location and consistent space use over extended periods. Floating individuals engage in nomadic exploration without permanent settlement, representing wandering movements, after exclusion as pack members, or individuals searching for mating opportunities; these movements show irregular displacement patterns with frequent directional changes [21,22]. Dispersal involves either short- or long-distance movements from (usually) natal territories to establish new territories or to join existing ones, characterised by sustained directional displacement [23].

Data collection and training data

Training segments were identified through expert classification based on visual inspection of movement trajectories and knowledge of individual life histories. The

training dataset comprised 23 segments from 13 individuals (Table 1; Additional file 1: Table S1).

Table 1. Training data composition for wolf behavioural classification.

Behavioural class	N segments	Selection criteria
Residency	13	Established territory holders with stable home ranges
Floating	5	Exploratory movements without site fidelity or directional persistence
Dispersal	5	Directed long-distance movements with a clear start/end

Number of expert-labelled training segments and the selection criteria applied to each movement strategy.

Behavioural profiles

Six movement metrics were calculated for each training segment: slope, R^2, rolling variance, volatility, reversal rate, and autocorrelation. The resulting behavioural profiles separated the three movement strategies, although not all metrics contributed equally (Table 2). Residency behaviour was characterised by near-zero slopes indicating minimal net displacement, low R^2 reflecting the absence of directional trends, and high reversal rates typical of oscillatory movements within a confined home range. Dispersal showed the opposite pattern, with high positive slopes, high R^2, low reversal rates, and high autocorrelation reflecting persistent directional movement. Floaters occupied an intermediate position, with near-zero slopes similar to residency segments but high rolling variance reflecting spatial instability, and reversal rates and autocorrelation intermediate between residency and dispersal, characteristic of erratic, non-directional exploration.

Table 2. Behavioural profiles for gray wolf movement strategies.

Metric	Residency	Floating	Dispersal
Slope	-0.20 ± 0.74	1.50 ± 2.51	2963.32 ± 2960.81
R^2	0.04 ± 0.04	0.05 ± 0.04	0.86 ± 0.06
Rolling variance	$4.35e^4$ ± $9.72e^4$	$1.68e^6$ ± $2.87e^6$	$2.11e^8$ ± $3.37e^8$
Volatility	88.79 ± 131.94	603.02 ± 833.88	3766.36 ± 4099.28
Reversal rate	0.59 ± 0.05	0.49 ± 0.07	0.32 ± 0.11
Autocorrelation	0.36 ± 0.22	0.65 ± 0.15	0.89 ± 0.03

Values are mean ± SD of each movement metric, calculated from expert-labelled training segments (n = 13 residency, 5 floating, 5 dispersal). SD: standard deviation.

Classification

We applied the classification framework to 31 wolves comprising 53 identified segments. Classification credibility, rated automatically from the overlap of bootstrap confidence intervals (see Classification and uncertainty quantification), was High for 35 segments (66.0%) and Medium for a further 9 (17.0%), together accounting for 83.0% of segments in which no class mean fell within the interval of an alternative strategy. The remaining segments were rated Low (7 segments, 13.2%) or Unclear (2 segments, 3.8%), indicating

overlapping class distributions that would warrant expert review (Additional file 1: Table S5; Additional file 2). The distribution of classified phases can be understood as reflecting the proportions in which animals in the studied population can be classified, with residency phases predominating and smaller proportions engaged in floating or dispersal behaviour: 31 residency phases (56.6%), 14 floating (26.4%), and 8 dispersal (15.1%).

As an illustrative example, wolf 103216 displayed a 356-day tracking record with two breakpoints partitioning the trajectory into three behavioural phases (Fig. 5, Table 3). Segment 1 (180 days, October 2024 – April 2025) was classified as residency with high credibility (65.0%, 95% CI: 55.8–74.4%), consistent with established territorial behaviour. Segment 2 (39 days, April – May 2025) represented a dispersal event (98.6%, 95% CI: 89.2–100.0%), reflecting directed long-distance movement. Segment 3 (136 days, May – October 2025) was classified as floating (95.1%, 95% CI: 83.4–98.2%). This sequence represents a typical life-history transition from natal territory through dispersal to settlement-seeking behaviour.

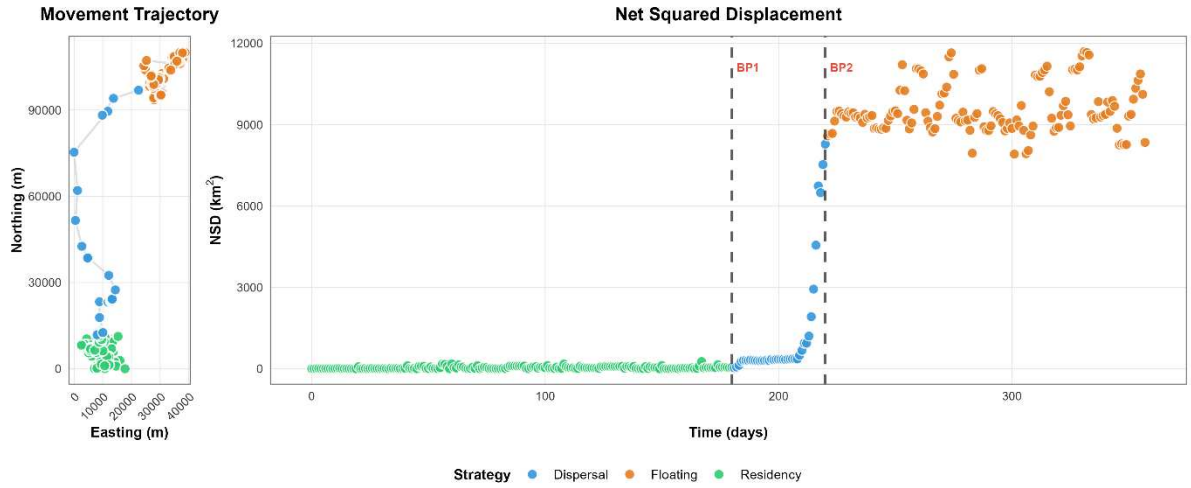


Figure 5. Movement trajectory and NSD time series for wolf 103216. The left panel shows spatial positions coloured by classified movement strategy. The right panel displays NSD over time with breakpoints separating three movement strategies: residency (green), dispersal (blue), and floating (orange).

Table 3. Classification results for wolf 103216.

Segment	Period	$P_{Residency}$	$P_{Floating}$	$P_{Dispersal}$	Class
1	22 Oct–20 Apr	65.0 [55.8, 74.4]	34.8 [25.4, 43.6]	0.3 [0.1, 0.7]	residency
2	21 Apr–30 May	0.0 [0.0, 0.0]	1.4 [0.0, 10.8]	98.6 [89.2, 100]	dispersal
3	31 May–14 Oct	3.0 [0.1, 14.9]	95.1 [83.4, 98.2]	1.9 [0.6, 3.7]	floating

Bootstrap probability estimates (mean [95% CI]) for each movement strategy across three trajectory segments. All three segments were rated High credibility (see Classification and uncertainty quantification). Credibility ratings for all classified segments are given in Additional file 1: Table S5.

Northern lapwing

Study species and movement strategies

Northern lapwings typically exhibit three distinct movement strategies that vary seasonally and across life-history stages. We defined three movement strategies based on expert classification. Residency phases encompass territory establishment, incubation, and chick-rearing with restricted movements around nest sites. Floating phases represent exploratory movements and migratory stopovers without directional persistence. Migration phases involve rapid, directed long-distance displacement between breeding grounds in Central Europe and wintering grounds in Spain and France. Distinguishing residency phases from floating behaviour proves particularly challenging, as both involve localised movements without sustained directional displacement [24].

Data collection and training data

GPS tracking data were collected from lapwings breeding in Czechia and migrating to wintering grounds in Spain and France between 2024 and 2026. Positions were aggregated into 12-hour centroids to capture the faster behavioural transitions typical of migratory birds. Training segments were identified through expert classification based on visual inspection of NSD trajectories and knowledge of breeding phenology. Nine segments containing fewer than five centroids were excluded, as very short segments yield unstable metric estimates. The training dataset therefore comprised 46 segments from four individuals, with all four individuals contributing segments to each behavioural class (Table 4; Additional file 1: Table S3), ensuring that profiles were not dominated by individual-specific movement patterns.

Table 4. Training data composition for northern lapwing behavioural classification.

Behavioural class	N segments	Selection criteria
Residency	10	Breeding individuals with restricted movements around nest sites during incubation and chick-rearing
Floating	27	Exploratory movements and stopovers without directional persistence
Migration	9	Rapid directed displacement between breeding and wintering grounds

Number of expert-labelled training segments and the selection criteria applied to each movement strategy. Nine segments containing fewer than five centroids were excluded.

Behavioural profiles

Five movement metrics were calculated for each training segment: absolute slope, R^2, rolling variance, volatility, and reversal rate. Because lapwings migrate in both directions between breeding and wintering grounds, the absolute slope was used rather than the signed slope applied to wolf trajectories. The resulting profiles separated migration sharply from the other two strategies, whereas residency and floating overlapped

substantially (Table 5). Migration was characterised by high absolute slope values, high volatility, low reversal rates, and high R^2, reflecting sustained directional displacement. Residency and floating phases showed similar metric values across most dimensions, consistent with the genuine ecological similarity between breeding site fidelity and stopover behaviour (Table 5).

Table 5. Behavioural profiles for northern lapwing movement strategies.

Metric	Residency	Floating	Migration
Absolute slope	4.94 ± 14.66	$1.75e^3 \pm 5.01e^3$	$1.25e^5 \pm 7.51e^4$
R^2	0.22 ± 0.20	0.34 ± 0.28	0.79 ± 0.15
Rolling variance	$5.03e^5 \pm 1.44e^6$	$6.50e^8 \pm 2.57e^9$	$6.44e^{10} \pm 9.15e^{10}$
Volatility	234.91 ± 597.30	$2.50e^3 \pm 4.10e^3$	$8.52e^5 \pm 3.48e^4$
Reversal rate	0.65 ± 0.14	0.59 ± 0.09	0.24 ± 0.16

Values are mean ± SD of each movement metric, calculated from expert-labelled training segments (n = 10 residency, 27 floating, 9 migration). SD: standard deviation.

Classification

We applied the classification framework to 78 segments across 11 individuals. Migration events were identified with high credibility, frequently achieving 100% probability with narrow confidence intervals. In contrast, residency and floating classifications typically showed probability distributions of approximately 50–55% versus 40–45%, reflecting genuine ecological overlap between these strategies (Additional file 1: Table S6; Additional file 3). Credibility was nonetheless High for 66 segments (84.6%) and Medium for 5 (6.4%), with the remaining 7 (9.0%) rated Low, indicating segments in which the interval of the assigned class contained the mean of an alternative and expert review would be warranted.

Classification confidence for residency and floating segments could be improved with larger training datasets, though the current uncertainty estimates accurately reflect the limits of the available training data. Experts familiar with lapwing ecology confirmed that distinguishing breeding residency from post-breeding floating represents a genuine challenge, consistent with why most movement studies in this species focus on the migration-residency dichotomy rather than finer classification [24].

As an illustrative example, individual 1300001473 displayed a 222-day tracking record partitioned into eight behavioural segments (Fig. 6, Table 6). The trajectory captured the complete annual movement cycle of a migratory lapwing, beginning with a residency phase during the breeding season (1 May–16 June), followed by an extended post-breeding floating phase (16 June–17 September). Autumn migration proceeded in three discrete bouts separated by floating stopovers of varying duration, ending with wintering-ground floating behaviour (20 November–9 December). Migration bouts were classified with high credibility, while residency and floating phases showed characteristic probability overlap. Despite this overlap, the confidence interval of each assigned class

was separated from those of all alternatives, and all eight segments were therefore rated High credibility, supporting the reliability of the classifications despite the behavioural similarity of the two strategies.

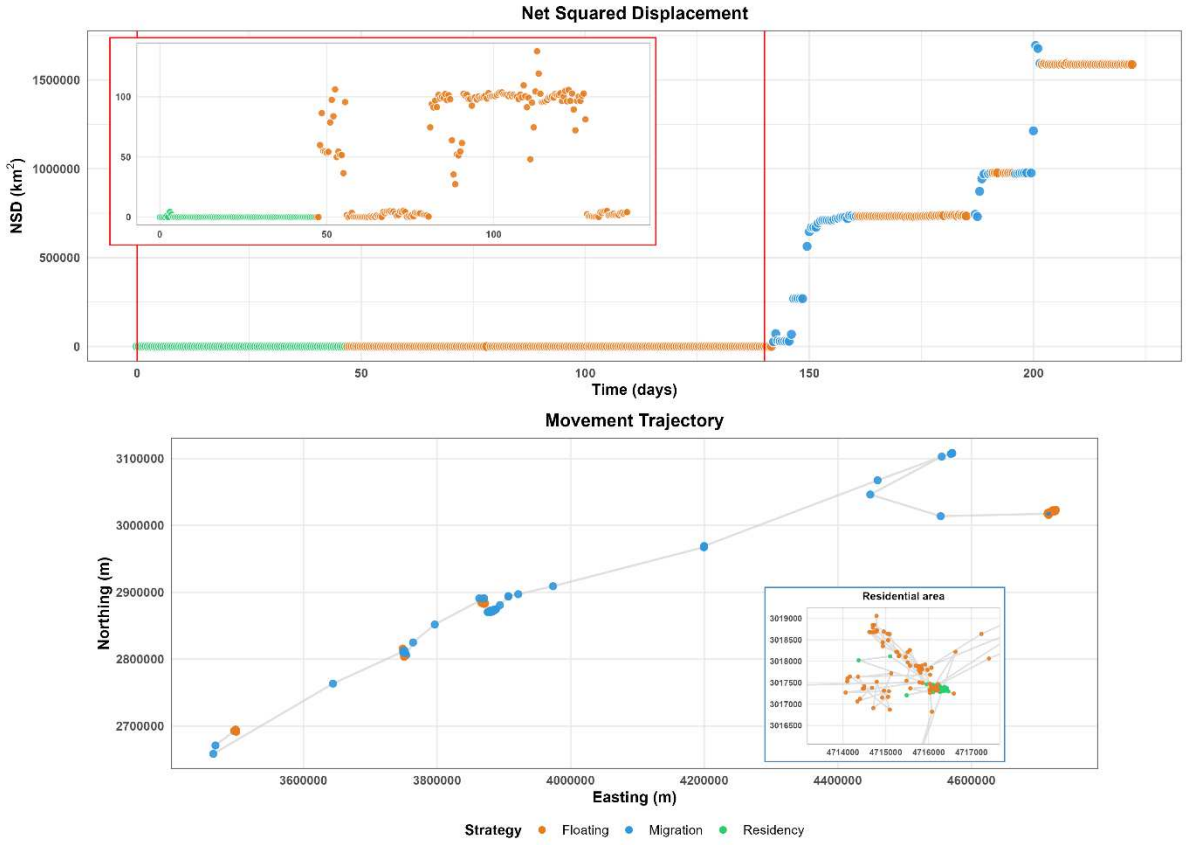


Figure 6. Movement trajectory and NSD time series for northern lapwing 1300001473. The lower panel shows spatial positions coloured by classified movement strategies. The upper panel displays NSD over time with three movement strategies: residency (green), migration (blue), and floating (orange).

Table 6. Classification results for northern lapwing 1300001473.

Segment	Period	$P_{Residency}$	$P_{Floating}$	$P_{Migration}$	Class
1	1 May–16 Jun	53.4 [52.1, 54.4]	43.6 [42.5, 45.0]	3.0 [2.6, 3.5]	residency
2	16 Jun–17 Sep	33.0 [8.6, 43.0]	62.6 [53.3, 85.5]	4.4 [3.5, 6.1]	floating
3	17 Sep–3 Oct	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	100 [100, 100]	migration
4	3 Oct–2 Nov	0.0 [0.0, 0.0]	90.5 [87.4, 93.2]	9.5 [6.8, 12.6]	floating
5	2 Nov–8 Nov	0.0 [0.0, 0.0]	2.6 [0.0, 25.7]	97.4 [74.3, 100]	migration
6	8 Nov–15 Nov	0.0 [0.0, 0.0]	91.9 [83.5, 94.7]	8.1 [5.3, 16.5]	floating
7	15 Nov–20 Nov	0.0 [0.0, 0.0]	0.2 [0.0, 0.0]	99.8 [100, 100]	migration
8	20 Nov–9 Dec	0.0 [0.0, 0.0]	93.7 [92.7, 94.7]	6.3 [5.3, 7.3]	floating

Bootstrap probability estimates (mean [95% CI]) for each movement strategy across eight trajectory segments. All eight segments were rated High credibility (see Classification and uncertainty quantification). Credibility ratings for all classified segments are given in Additional file 1: Table S6. CI: confidence interval.

Discussion

Classifying animal movement strategies from tracking data remains a challenge in movement ecology. Existing approaches often require either strong parametric assumptions about trajectory shape or extensive labelled datasets for machine learning [4,17], creating barriers for researchers working with novel species, limited sample sizes, or limited statistical expertise, as telemetry is increasingly used outside the professional scientific community. The profile-based framework presented here offers an alternative option: empirically derived behavioural profiles, distance-based classification, and bootstrap uncertainty quantification that together provide reliable, interpretable results while remaining accessible to ecologists without specialised statistical training.

Our simulations provide practical advice: reliable classification does not require large training sets. Accuracy improved between two and five segments per class considerably and then plateaued, with little gain beyond ten. A carefully curated set of 5 to 10 unambiguous examples per movement strategy, chosen by expert judgement or independent validation, is therefore sufficient, so researchers need not delay classification until extensive training data have accumulated. Segment duration matters because strategies differ in how quickly their signal accumulates. Dispersal is identifiable from short segments, whereas residential and floating require longer series, since separating them depends on observing repeated reversals and local variance that stabilise only over weeks. For large mammals tracked at daily resolution, this implies minimum segment durations of 30 to 60 days; shorter segments remain usable but yield wider confidence intervals.

The simulation errors were strongly asymmetric, and this asymmetry is mechanistically informative. Residential segments were misclassified as floating far more often than the reverse, because residential trajectories include excursions (hunting forays, territorial patrols) that, sampled in isolation, resemble floating, whereas floating rarely mimics the consistent return-to-centre pattern of residency. Dispersal was almost never confused with either, reflecting its distinct directional NSD dynamics. These simulated patterns mirror our empirical results: wolves separated cleanly between residency and dispersal, while lapwings showed genuine residency-floating overlap that experts confirmed as real ecological ambiguity rather than methodological failure.

Our framework also differs from existing approaches in flexibility, interpretability, and training-data requirements. Parametric NSD models assume trajectories follow predefined functional forms (typically asymptotic curves for migration or dispersal), an assumption that fails for complex or variable movement and struggles with floating's high NSD variance; our profile-based approach instead learns metric distributions directly from training data, imposing no functional form [4,13,15]. Hidden Markov Models require specifying transition and emission probabilities that are difficult to justify for species with

limited prior characterisation [25–27] while machine learning needs larger training datasets than most movement ecologists possess and is less interpretable [16,17]. The framework thus occupies a useful middle ground: more flexible than parametric fitting, more interpretable than machine learning, and less assumption-heavy than HMMs.

The cross-taxa case studies demonstrate that this flexibility translates into practical utility. Wolf and lapwing movement occur on fundamentally different scales: wolf dispersal slopes averaged 2,963 km^2 per day while lapwing migration slopes reached 125,190 km^2 per day, a nearly 40-fold difference. Yet the same methodological framework, parameterised with species-appropriate training data, achieved reliable classification in both systems [3]. This adaptability reflects a key design principle: rather than hard-coding thresholds or functional forms, the framework learns what distinguishes movement strategies in each specific context. A slope that signals directed movement in one species may fall well within the range of localised movement in another; the profile-based approach handles both cases by referencing empirical training distributions rather than fixed values.

The bootstrap confidence intervals, while a standard tool for uncertainty quantification, serve as an additional diagnostic function in this framework. Wide confidence intervals for short segments do not indicate methodological failure; they honestly acknowledge that brief observation periods contain insufficient information for confident classification. Similarly, overlapping probabilities for behaviourally similar strategies (residency versus floating in lapwings) reflect genuine ecological ambiguity. Where the interval of the assigned class contains the mean of an alternative, the credibility rating flags the segment as Low, providing valuable information: this trajectory does not clearly belong to either category. Researchers can use such signals to flag segments requiring additional information (e.g., reproductive status, proximity to nest sites) or to acknowledge uncertainty in downstream analyses rather than propagating false confidence.

Based on our simulation experiments and empirical experience, we offer the following guidelines for researchers implementing this framework. A key advantage of this framework is reliable classification with relatively small training samples, compared to hundreds of segments typically required for machine learning approaches, though the minimal sample size depends on the complexity of the behaviours and their degree of separation in metric space. We recommend assembling at least 5–10 unambiguous training segments per movement strategy and examining metric distributions before finalising metric selection, as not all metrics contribute equally across classification tasks.

Several limitations warrant acknowledgement. Classification quality depends entirely on training data quality; unrepresentative or mislabelled training segments will produce unreliable profiles. The framework assumes identified segments represent relatively

homogeneous movement patterns, an assumption that may be violated during rapid behavioural transitions. Optimal metric selection requires exploratory analysis and some degree of ecological judgement, introducing subjectivity into an otherwise algorithmic process. While bootstrap confidence intervals provide useful uncertainty estimates, they do not account for all sources of error, particularly systematic biases in GPS positioning or temporal autocorrelation in location data.

Future development should address several promising directions: real-time classification for adaptive wildlife management and extension to three-dimensional movement data from marine or aerial tracking. The integration of profile-based classification with step selection functions is a particularly natural next step: in a companion study, we use the movement strategies classified here as the basis for an integrated step selection analysis of wolf habitat selection, showing that resident, dispersing, and floating wolves select habitat differently across human-dominated landscapes (Kadlec et al., unpublished data). An R package (*moveprofile*) implementing the complete framework is available at https://github.com/kadleci/moveprofile.

Conclusion

The profile-based framework presented here provides an interpretable, flexible, and uncertainty-aware approach to classifying different animal movement strategies from tracking data. We showed that reliable classification can be achieved with as few as 5 to 10 training segments per movement strategy, a feasible sample size for most typical telemetry studies. The same framework transfers across taxa with very different spatial and temporal scales, provided that the training data are appropriate. Bootstrap confidence intervals serve as diagnostic indicators of genuine ecological ambiguity rather than mere statistical noise, flagging cases where movement patterns are hard to distinguish.

We emphasise that this framework does not replace a deeper mechanistic understanding of animal movement; rather, it provides a standardised, reproducible foundation for the analyses that build on movement classification. By making reliable classification accessible without requiring extensive statistical expertise, we hope to lower barriers for movement ecologists seeking to extract behavioural insight from increasingly abundant tracking data.

List of abbreviations

AIC: Akaike Information Criterion

CI: confidence interval

GPS: Global Positioning System

HMM: Hidden Markov Model

NSD: Net Squared Displacement

SD: standard deviation

Declarations

Animal Ethics declaration

All capture, handling and GPS tagging procedures were approved by the relevant national and regional authorities listed below, and were carried out in accordance with applicable institutional, national and international guidelines for the treatment of animals in research. Ethical approval was granted under the permits specified below and detailed in Additional file 1: Table S7.

Ethics approval and consent to participate

This study involved capture and GPS tagging of wild gray wolves and northern lapwings for telemetry purposes; no additional experimental manipulation was performed, and all procedures followed applicable institutional, national and international ethical standards. Wolf trapping in Czechia was authorised by the Ministry of the Environment (permits MZP/2018/630/2582, MZP/2022/630/929, SR/0012/US/2021-5, MZP/2022/630/735), national park and nature conservation authorities (NPS 08816/2020/4, SZ SNPCS 00118/2022, KUUK/049576/2022, Krkonoše NP 01273/2021 and 09508/2023, Implementation Contract of 16 August 2021), in Austria by the Government of Lower Austria (LF1-TVG-59/001-2018), and in Germany by the Animal Welfare Authorities of Mecklenburg-Western Pomerania (7221.3-1-1-056/11-1, 7221.3-1-027/15, 7221.3-1-046/20), the German Armed Forces (42-34-30-20 G02-24) and Saxony-Anhalt (203.m-42502-2-1686 TUDD G). Northern lapwing capture was carried out under a ringing licence from the National Museum in Prague (Licence no. 1082) and municipal authorities in Hradec Králové, Holice and Pardubice (MMHK/254806/2024, MUHO 10216/2024/OŽP/Po, SZ_MMP 55492/2024, respectively). Full details are provided in Additional file 1: Table S7.

Consent for publication

Not applicable.

Availability of data and materials

The *moveprofile* R package, implementing the complete workflow, is provided as Additional file 4 and is also available on GitHub (https://github.com/kadleci/moveprofile) and archived at Zenodo (https://doi.org/10.5281/zenodo.XXXXXXX). The analysis scripts reproducing the simulation study and both case studies are provided as Additional file 5. A reproducible worked example, based on a selected subset of the wolf tracking data with spatial coordinates translated to a relative origin, is included in the package as a vignette. The full GPS tracking data underlying the results are not publicly available because both study species are of conservation concern, and precise location data could facilitate persecution or disturbance. The data are archived under restricted access at Zenodo (https://doi.org/10.5281/zenodo.21641592) and are available upon request, subject to approval by the respective data owners.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

I.K. conceived the study, developed the profile-based framework and the *moveprofile* R package, performed the analyses, produced the figures, and wrote the original draft. J.S. contributed methodological ideas, co-developed the package, and helped write the manuscript. A.V., V.B. and J.S. supervised the work. A.V., M.K., M.D., A.S., V.M.-H. and N.S. collected the wolf tracking data, and M.S. and L.B.P. the northern lapwing data. I.K. prepared and curated the wolf dataset, and L.B.P. the lapwing dataset. A.V., M.S., M.K., M.D., N.S. and V.M.-H. acquired the funding under which the data were collected. All authors read and approved the final manuscript.

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Additional files

Additional file 1. Supplementary tables (DOCX). Table S1. Individuals used for profile construction in the gray wolf case study. Table S2. Individuals classified in the gray wolf case study. Table S3. Individuals used for profile construction in the northern lapwing case study. Table S4. Individuals classified in the northern lapwing case study. Table S5. Classification results for all gray wolf segments. Table S6. Classification results for all northern lapwing segments. Table S7. Permit details for data collection.

Additional file 2. Interactive NSD time series and classified movement strategies for all gray wolves (HTML).

Additional file 3. Interactive NSD time series and classified movement strategies for all northern lapwings (HTML).

Additional file 4. *moveprofile* R package, version 0.1.0, source distribution, distributed under the GNU General Public License version 3 (TAR.GZ).

Additional file 5. Analysis scripts reproducing the simulation study and both case studies (ZIP).

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