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MoveFormer: a Transformer-based model for step-selection animal movement modelling

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Abstract

The movement of animals is a central component of their behavioural strategies. Statistical tools for movement data analysis, however, have long been limited, and in particular, unable to account for past movement information except in a very simplified way. In this work, we propose MoveFormer, a new step-based model of movement capable of learning directly from full animal trajectories. While inspired by the classical step-selection framework and previous work on the quantification of uncertainty in movement predictions, MoveFormer also builds upon recent developments in deep learning, such as the Transformer architecture, allowing it to incorporate long temporal contexts. The model predicts an animal's next movement step given its past movement history, including not only purely positional and temporal information, but also any available environmental covariates such as land cover or temperature. We apply our model to a diverse dataset made up of over 1550 trajectories from over 100 studies, and show how it can be used to gain insights about the importance of the provided context features, including the extent of past movement history. Our software, along with the trained model weights, is released as open source.

Contents

1 Introduction

The movement of animals is a central component of their behavioural strategies to best exploit the landscape they live in, to find a mate or to avoid predators, for instance. The role that these movements have beyond the individual, for instance in shaping animals' ecosystem impacts, is clear. Accordingly, and thanks to the technological developments that are allowing to collect more detailed movement data on more individuals and species each day, the study of animal movement has become an important goal of ecology [1].

For a long time, however, statistical tools to analyze movement data were lacking or limited. Over time, though, purely pattern-based descriptions (e.g. home-range analyses) have been complemented by regression models allowing to infer the effects of spatio-temporal features on movement. *Step-selection function* (SSF) models, which compare actual movement steps with realistic candidate ones, are one of such models and have de facto become the established approach to analyse animal trajectories [2–4]. They are now routinely used to infer and quantify the effect of environmental variables such as, for instance, land cover or temperature.

However, an animal's movement is likely to be driven not only by spatio-temporal environmental features, but also by some internal knowledge and rules that are unobservable directly. The importance of memory and of an animal's familiarity with places is increasingly recognized [5–7], and familiarity is usually incorporated into SSF models using a *previously visited* yes/no variable, or a *time-spent* variable, often calculated over an arbitrary time window [8, 9]. Memory of places and their characteristics can also lead to routine movement behaviours. Traplining, in which an individual travels to the same places in the same order, is rare, but it is clear from visual inspection of animal trajectories that many animals display some form of routine movement behaviours. But for traplining, which has received a lot of interest, the study of routine movement behaviour has remained extremely limited [10]. Riotte-Lambert et al. [11] showed how conditional entropy, calculated using the information on visits to patches, could be used as a metric of routine in movement. That metric has not been used much since then, possibly because the need to determine sites may render its application difficult on data collected in nature, where patches can be difficult to determine, be diffuse, or not exist at all. Further work is needed to describe and explain routine movements, which result from the interaction between memorized knowledge, movement rules and environmental context. Additionally, we are not aware of any work that has focused on how to incorporate complex information about past movement and environmental context into predictive models of animal movement, although it should, by definition, improve predictions. The question: 'To what extent past movements inform where an animal is likely to go next?' remains open.

The classic implementation of the SSF framework appears unsuitable to address this difficult question. We therefore developed a new type of model that we named MoveFormer. We conserved the conceptual attractiveness of SSF, but built on the most recent developments in deep learning to embed the information about current and past animal location, movement and environmental context.

Our contribution is threefold. First, we propose a model that learns to best predict the next step of a movement trajectory based on a given context length, i.e. a given time-window of information about the past. Second, the proposed approach is flexible enough to allow each step in the context to be defined not only by the locations of the start and end points, but also by any kind of features that could be relevant, in particular environmental variables. Third, we show how the model can be used to gain insights about the importance of the provided context, both in terms of the extent of the past that it is useful to know, and in terms of what kinds of information are most ecologically relevant to predict an animal's movement. We demonstrate this by comparing the predictions, via information-theoretic metrics and prediction accuracy, for different context lengths or with randomized features. Model training and analyses are conducted on a dataset made up of over 1550 trajectories from over 100 studies, encompassing various species within mammals, birds and reptiles.

The MoveFormer source code, including code for data pre-processing and evaluation, as well as complete hyperparameter settings, is available online.[1] We also release the weights of the trained models.[2]

2 Data

In this section, we describe our sources of data, specifically: movement data (trajectories consisting of latitudes, longitudes and timestamps), geospatial variables (associated with locations), and taxonomic classification information (associated with each animal).

2.1 GPS location data

Our main source of location data is Movebank[3] [12], an online repository for animal movement data. The location data in Movebank is presented as latitude/longitude pairs along with UTC timestamps and is grouped into trajectories (*deployments*) and associated with (occasionally missing) metadata such as a taxon name, sex, and date of birth. We used the Movebank API to retrieve data from GPS sensors for all 269 studies that were available[4] for download under a Creative Commons[5] license (CC0, CC BY and CC BY-NC), obtaining 13 577 trajectories comprising a total of 197 million observations (location events). We subsampled the trajectories (splitting them into segments when necessary) so that observations occur at midnight and at noon (according to local mean time) with a tolerance of ±3 h and so that the time difference between consecutive observations is 9 to 15 h. We discarded trajectory segments shorter than 120 observations, leaving us with 1440 trajectories from 98 different studies [13–165]. See Table 4 in the appendix for the full list of studies and their licenses.

We added unpublished data from 4 more studies, collected by one of us (S.C-J). These are GPS data from plains zebras and African elephants, collected in Hwange National Park (Zimbabwe), and GPS data from plains zebras and blue wildebeest, collected in Hluhluwe-iMfolozi Park (South Africa). After subsampling and filtering as in the case of the Movebank data, we obtained 73 trajectories.

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[1] `https://github.com/cifkao/moveformer`

[2] `https://doi.org/10.5281/zenodo.7698263`

[3] `www.movebank.org`

[4] as of 15 February 2022

[5] `https://creativecommons.org/`

section		#spec	#ind	#traj	#obs
train		61	1383	2786	915618
val		17	53	133	50984
test		21	70	133	40334
class	**order**	#spec	#ind	#traj	#obs
Aves		*39*	*895*	*1915*	*640420*
	Accipitriformes	10	138	315	65189
	Anseriformes	10	169	210	69386
	Bucerotiformes	1	5	6	4448
	Cathartiformes	1	12	34	8965
	Charadriiformes	10	310	585	235722
	Ciconiiformes	2	249	751	253541
	Gruiformes	1	1	1	189
	Passeriformes	1	3	3	474
	Pelecaniformes	1	6	6	1764
	Struthioniformes	1	1	1	221
	Suliformes	1	1	3	521
Mammalia		*15*	*439*	*845*	*290789*
	Artiodactyla	7	329	660	218698
	Carnivora	6	41	51	12404
	Perissodactyla	1	26	34	25582
	Proboscidea	1	43	100	34105
Reptilia		*6*	*58*	*116*	*40353*
	Testudines	6	58	116	40353

Table 1: Number of species, individuals, trajectories, and observations in each section of the dataset, and a breakdown by taxa.

The final dataset contains about 1 million observations from 1506 individuals, grouped into 1513 trajectories with a median length of 408. We performed a train/validation/test split, making sure that 1) the validation and test sections contain only frequent species (with at least 10 members in the full dataset), and 2) each individual appears in exactly one split. Table 1 details the amounts of data by section and by taxonomic classification and Fig. 1 shows the geographical distribution.

During training and evaluation, we additionally split each trajectory into segments of length $N_{\max} = 500$ and subsequently consider each of these segments as a separate trajectory.

2.2 Taxon vectors

Each trajectory in our data is associated with a taxon name (most commonly the animal's species). To obtain a dense vector representation of the taxon, we look up its Wikipedia article and retrieve the associated 100-dimensional embedding vector from Wikipedia2Vec [166].

A property of Wikipedia2Vec is that embeddings of semantically similar entities are placed close together in the embedding space. To illustrate that this

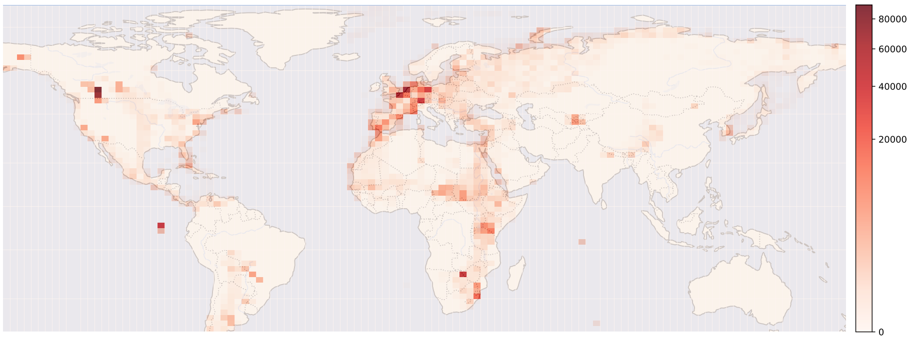

Figure 1: The geographical distribution of the observations in the dataset.

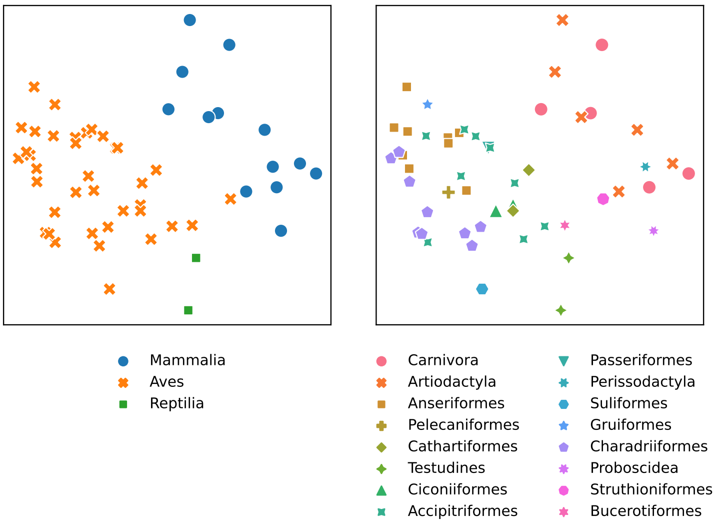

Figure 2: A PCA projection of Wikipedia2Vec embeddings of species, labeled by class (left) and order (right).

extends, to some degree, to similarity between species, we display in Fig. 2 the PCA (principal component analysis) projections of species embeddings, labeled by higher taxonomic ranks. We also measured the cosine similarity between all pairs of embeddings and found it to be correlated with the number of common ancestors of the two species in the taxonomic hierarchy (Spearman $\rho = 0.68$).

Overall, the Wikipedia2Vec embeddings appear to meaningfully encode a species' position in the phylogeny. Hence, we speculate (though we do not test this in the present work) that their inclusion in the model should help this model to generalize to species that are not present in the training data, at least as long as they are sufficiently similar to those that are.

2.3 Geospatial variables

The proposed model is powerful enough to account not only for each trajectory intrinsic dynamics but also for any *third-party* additional information that may be available as covariates. In order to illustrate this, we augment each trajectory data point with exogenous information. For each location, we retrieve the following geospatial variables, which could be ecologically relevant, from publicly available raster data:

- 2009 Human Footprint, 2018 Release [167, 168] (resolution: ~1 km); we normalize the values between 0 and 1 and sample them with bilinear interpolation;
- 19 bioclimatic variables from WorldClim 2.1 [169] (resolution: ~1 km); we standardize the values (zero mean, unit variance) and use nearest neighbor interpolation;
- land cover classification (23 classes) from Copernicus Global Land Service, version 3.0.1, epoch 2015 [170] (resolution: ~100 m); we use a one-hot encoding and nearest neighbor interpolation.

3 Model

Formally, we consider the dataset as composed of *trajectories*, where a trajectory[6] $\xi_{1\ldots N}$ of length N consists of locations $x_{1\ldots N}$, corresponding to timestamps $t_{1\ldots N}$, and any associated variables $z_{1\ldots N}$, i.e. $\xi_n = (x_n, z_n, t_n)$ as described above. Our main goal is to estimate a model for the next-step prediction task, i.e. for any given $n \in \{1,\ldots,N\}$, predict the next location x_{n+1} from the trajectory prefix $\xi_{1\ldots n}$ and the next timestamp t_{n+1}.

As a fundamental use case, we are interested in analyzing the effect of available past context on the prediction of x_{n+1}. Specifically, for a varying *context length* $c \in \{1,\ldots,c_{\max}\}$ (where $c_{\max}$ is an arbitrary constant), we wish to study the behavior of the prediction of x_{n+1} given $\xi_{n-c+1\ldots n}$ and t_{n+1}. Hence, we are in fact interested in a model accepting as input any *trajectory segment* of length at most $c_{\max}$, and predicting the next location.

We adopt a step-selection function modelling approach [2, 4], based on selecting the end-point location of a step from a set of candidates. Specifically, for a position $n+1$ within a trajectory, given an associated timestamp t_{n+1}, a set of candidate locations $x_{n+1}^{(1\ldots K)}$ and associated variables $z_{n+1}^{(1\ldots K)}$, we are interested in estimating a probability distribution over the candidates:

$$P\Big(y_{n+1} = i \;\Big|\; \xi_{1\ldots n}, t_{n+1}, x_{n+1}^{(1\ldots K)}, z_{n+1}^{(1\ldots K)}\Big), \tag{1}$$

where $i \in \{1,\ldots,K\}$.

We propose to model this distribution using a deep neural network, consisting of a *Transformer* [171] *encoder* and a *candidate selection module*, as depicted in Fig. 3. The role of the Transformer is to encode the trajectory up until position n, i.e. $\xi_{1\ldots n}$ along with the timestamp for the next observation, t_{n+1}. The candidate selection module then encodes each candidate $x_{n+1}^{(i)}$ and employs an attention mechanism to compute a probability distribution over the candidates. The model is described in detail in Section 3.1, followed by our choice of input representation in Section 3.2.

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[6] We use $\xi_{1\ldots N}$ as shorthand notation for the sequence $\xi_1, \xi_2, \ldots, \xi_N$. Note that N may be different for each trajectory in the dataset.

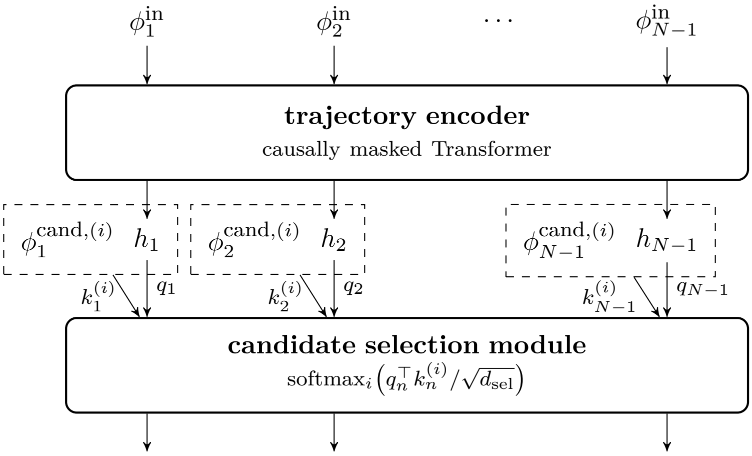

Figure 3: The high-level architecture of MoveFormer. The input to the trajectory encoder is a sequence of embedding vectors $\phi_{1\ldots N-1}^{\text{in}}$, each corresponding to a different data point (location-timestamp pair) in the trajectory. The encoder outputs a sequence of vectors $h_{1\ldots N-1}$; the causal masking in the encoder causes each h_n to encode only the inputs up to position n, i.e. $\phi_{1\ldots n}^{\text{in}}$. This representation is then fed to the candidate selection module, which uses it as *queries* in an attention mechanism that assigns probabilities to different candidate locations. Both the input embeddings $\phi_{1\ldots N-1}^{\text{in}}$ and the candidate embeddings $\phi_n^{\text{cand},(i)}$ are computed through embedding layers which are not displayed here but described in Section 3.1.1.

In order to train and evaluate this model, we also need a way to generate suitable candidate locations $x_{n+1}^{(i)}$. We use a simple but general method employing quantile-based modelling of turning angles and movement distances, as detailed in Section 3.3.

3.1 Step-selection model

3.1.1 Input embeddings

We build two sets of embeddings $\phi_n^{\text{in}}, \phi_n^{\text{cand},(i)} \in \mathbb{R}^{d_{\text{emb}}}$, $n \in \{1, \ldots, N-1\}$, $i \in \{1, \ldots, K\}$ such that:

- ϕ_n^{in}, input for the trajectory encoder, depends on $x_{n-1}, x_n, t_n, t_{n+1}, z_n$;
- $\phi_n^{\text{cand},(i)}$, input for the candidate selection module, depends on $x_n, x_{n+1}^{(i)}, z_{n+1}^{(i)}$.

The inputs are represented as collections of carefully engineered continuous and discrete features that we will describe later (see Section 3.2). Missing (NaN) values are replaced with a special embedding vector learned as an additional parameter. In each case, we project each feature vector to a common embedding space $\mathbb{R}^{d_{\text{emb}}}$, then linearly combine them (with different learnable coefficients in each of the two cases).

More precisely, for ϕ^{in}:

$$\phi_n^{\text{in}} = \sum_{j=1}^{F} w^{\text{in},(j)} \left(W^{(j)} f_n^{(j)} + b^{(j)} \right), \tag{2}$$

where $f_n^{(j)}$ is the j-th out of all F feature vectors at step n, and the learnable parameters are coefficients $w^{\text{in},(j)} \in \mathbb{R}$ (we set $w^{\text{in},(j)} = 0$ for features we do not wish to consider), biases $b^{(j)} \in \mathbb{R}^{d_{\text{emb}}}$ and weight matrices $W^{(j)} \in \mathbb{R}^{d_{\text{emb}} \times d_j}$. The formula for $\phi_n^{\text{cand},(i)}$ is analogous. As can be seen from Eq. (2), the chosen method for constructing input embeddings allows features to have different dimensions and automatically projects them to the desired embedding dimension (via $W^{(j)}$ and $b^{(j)}$) before applying scaling through $w^{\text{in},(j)}$.

3.1.2 Trajectory encoder

The trajectory encoder is a Transformer encoder with causally masked attention. It receives the embedding sequence $\phi_{1...N-1}^{\text{in}}$ and outputs a sequence of vectors $h_{1...N-1}$ where h_n is a representation of $\xi_{1...n}$. The encoder does not use any positional encoding in the conventional sense (encoding the indices $1, \ldots, N-1$, as is commonly done in Transformers), but position information is conveyed by the feature representations of the timestamps $t_{1...N-1}$.

3.1.3 Candidate selection

The candidate selection module is used to select the next location out of a list of candidates. We build upon the common approach that models the probability of an individual being present at a given candidate location via conditional logistic regression [3]; expressed in our notation:

$$\frac{\exp\left(\beta^\top \phi_n^{\text{cand},(i)}\right)}{\sum_{i'=1}^{K} \exp\left(\beta^\top \phi_n^{\text{cand},(i')}\right)}, \tag{3}$$

where β is a parameter vector.

In this work, in order to incorporate the context representation computed by the trajectory encoder, we replace the global parameter vector β with a context-dependent *query vector* $q_n \in \mathbb{R}^{d_{\text{sel}}}$, which is a linear projection of the trajectory encoder output h_n. We also do not use the raw candidate features $\phi_n^{\text{cand},(i)}$ but replace them with a *key vector* $k_n^{(i)} \in \mathbb{R}^{d_{\text{sel}}}$, which is computed by concatenating the feature vector with the corresponding encoder output h_n and passing the result through a *candidate encoder* (a fully-connected network): $k_n^{(i)} = E_{\text{cand}}([\phi_n^{\text{cand},(i)}, h_n])$. Thus, we arrive at a *dot-product attention mechanism*; scaling the dot products by $1/\sqrt{d_{\text{sel}}}$ as in Transformer attention [171], we have:

$$P\left(y_{n+1} = i \,\middle|\, \xi_{1...n}, t_{n+1}, x_{n+1}^{(1...K)}, z_{n+1}^{(1...K)}\right) = \frac{\exp\left(q_n^\top k_n^{(i)} / \sqrt{d_{\text{sel}}}\right)}{\sum_{i'=1}^{K} \exp\left(q_n^\top k_n^{(i')} / \sqrt{d_{\text{sel}}}\right)}. \tag{4}$$

During training, the first candidate location $x_{n+1}^{(1)}$ is taken as the true next location x_{n+1}; the rest of the candidates are randomly sampled around the current location x_n (we detail this process below). This allows us to define a cross entropy loss, which we minimize through stochastic gradient descent using the Adam optimizer:

$$\mathcal{L} = -\frac{1}{N-1} \sum_{n=1}^{N-1} \log_K P\Big(y_{n+1} = 1 \,\Big|\, \xi_{1\ldots n}, t_{n+1}, x_{n+1}^{(1\ldots K)}, z_{n+1}^{(1\ldots K)}\Big) \tag{5}$$

3.1.4 Variable receptive field training

As mentioned above, we aim to evaluate our model on arbitrary trajectory segments up to some maximum length $c_{\max}$ (this procedure is detailed below in Section 4.1). As can be seen from Eq. (5), our model is effectively being simultaneously trained on all prefixes of the trajectory $\xi_{1\ldots N}$. Hence, the model is able to accept segments of variable length as desired, but being only trained on trajectory prefixes may bias it, leading to incorrect predictions on segments that are not prefixes. To alleviate this, we propose a training scheme that intervenes on the attention weights to randomly vary the past context available for each prediction.

In each training batch, we sample a random integer B uniformly from $\{1, \ldots, N_{\max}\}$ and apply a block-diagonal attention mask to the attention matrix (on top of the causal mask) with blocks of size B (with the last block truncated if $B \nmid N$). As a result, the ranges of positions $\{1, \ldots, B\}$, $\{B+1, \ldots, 2B\}$, etc. are prevented from attending to each other, and the corresponding segments are therefore effectively considered as separate trajectories.

3.2 Data representation

Let us now describe the feature mappings used for location and time, as well as associated features.

3.2.1 Location

In the raw data, each location x_n is represented as a GPS coordinate pair (latitude, longitude). We represent it as a geodetic normal vector (*n-vector*) $\nu(x_n) \in \mathbb{R}^3$.

Additionally, we encode the position relative to the previous location x_{n-1} as a *movement vector* $\mu(x_{n-1}, x_n) \in \mathbb{R}^2$, obtained by computing the bearing and distance from x_{n-1} to x_n and converting them to cartesian coordinates. We apply scaling to make the overall root-mean-square (RMS) of the norms of movement vectors computed on the training dataset equal to 1.

Analogously, we encode each candidate location $x_{n+1}^{(i)}$ as an n-vector $\nu(x_{n+1}^{(i)})$ and as a movement vector $\mu(x_n, x_{n+1}^{(i)})$.

3.2.2 Time

We encode a timestamp t_n as:

- a 10-dimensional vector of sines and cosines with a period of 1 second, 1 minute, 1 hour, 1 day, and 1 tropical (solar) year, respectively, such that their phase synchronizes on January 1st, 2000, at 00:00:00 UTC;
- $\sin(\mathrm{LMT}/24 \cdot 2\pi)$ and $\cos(\mathrm{LMT}/24 \cdot 2\pi)$, where LMT is the local mean time (i.e. UTC adjusted by longitude) in (fractional) hours;
- 3 integer values (one-hot-encoded) representing the calendar month (0–11), the day of the month (0–30), and the day of the week (0–6) in UTC.

We also encode the time difference w.r.t. the next timestamp t_{n+1} as a 12-dimensional vector of sines and cosines with the same periods as above, plus a period of 25 years. While this multi-scale encoding may not be necessary in our case (where the time differences are between 9 and 15 h), we propose it as a generic representation suitable for any time scale from seconds to years (and hence for virtually all existing animal movement data).

3.2.3 Associated variables

For each input and candidate location, we retrieve and pre-process geospatial variables as described in Section 2.3. We also include the taxon vectors (as described in Section 2.2) as an additional encoder feature vector for every element of the input sequence.

3.3 Candidate sampling

We sample each candidate location $x_{n+1}^{(i)}$ as follows:

- we estimate the current bearing β of the animal from the positions x_n and x_{n-1};
- we independently sample a *turning angle* $\theta \sim \hat{P}(\theta)$ and a *log-distance* $\log d \sim \hat{P}(\log d)$; $\beta' \leftarrow \beta + \theta$;
- we compute $x_{n+1}^{(i)}$ by moving x_n according to β' and d.

$\hat{P}(\theta)$ and $\hat{p}(\log d)$ are estimated on the training set as follows:

- We collect all turning angles from the training set and compute the quantiles (estimated using linear interpolation) at 101 equally spaced points $0 = q_0, q_1, \ldots, q_{100} = 1$. We use them to construct the quantile function of $\hat{P}(\theta)$ as a piecewise linear function with knots at $q_0, q_1, \ldots, q_{100}$.
- We collect the natural logarithms of all non-zero distances between consecutive points in the dataset; we construct the quantile function of $\hat{P}(\log d)$ analogously.

We sample from each distribution by drawing a sample from $\mathcal{U}[0, 1]$ and passing it through the estimated quantile function; this is sometimes called the *increasing rearrangement* [172].

In our experiments, we condition the distributions on the taxon, i.e. we estimate a separate pair of distributions on the section of the training dataset corresponding to each taxon.

3.4 Implementation details and hyperparameters

Our implementation of MoveFormer, available as open source software,[7] is written in Python using the PyTorch framework[8] and the `x-transformers`[9] package. The code for efficient geospatial variable loading relies on the `rasterio`[10] library and is released as a separate package, `gps2var`.[11]

The trajectory encoder is a 6-layer Transformer with 8 attention heads per layer and a feature dimension of 128. The candidate encoder is a fully-connected neural network with one hidden layer of size 256 and a GELU activation [173]. The candidate selection module has $d_{\text{sel}} = 128$. The total number of parameters of the model is around 2.6 million – several orders of magnitude smaller than current state-of-the-art Transformer language models, for instance, but appropriate for the limited-size dataset that we are working with.

The Adam optimizer uses a learning rate of 5×10^{-5} with linear warm-up and exponential decay. We train for 180 epochs with a batch size of 24, taking 7.5 h on a Tesla V100 GPU (note that GPU utilization was only about 20 % and the performance bottleneck appeared to be the geospatial variable loading). We validate on the validation set twice per epoch and use the checkpoint with the lowest validation loss.

The complete hyperparameter settings are included with the source code.

4 Analysis methods

4.1 Context length analysis

Riotte-Lambert et al. [11] propose to use *conditional entropy* as a measure of uncertainty in predicting the next location given the c previous locations. Specifically, given a distribution P over sequences of locations, conditional entropy of order c can be written as

$$H_c = -\mathbb{E}_{P(s_1,\ldots,s_c)}[\log P(s_{c+1} \mid s_1,\ldots,s_c)], \tag{6}$$

where $P(s_1,\ldots,s_c)$ is understood as the probability of c consecutive locations in a sequence being equal to $s_1,\ldots,s_c$, and $P(s_{c+1} \mid s_1,\ldots,s_c)$ as the conditional probability of s_{c+1} immediately following the sequence $s_1,\ldots,s_c$. Considering this uncertainty measure as a function of the context length c, it may be used to study routine movement behavior.

Riotte-Lambert et al. [11] work with a finite set of discrete locations, allowing them to evaluate the expression (6) empirically on a given trajectory. However, the probability estimates quickly become unreliable with increasing c due to data sparsity. Moreover, the method is inapplicable when locations are unique, as in our case.

We propose an alternative way, which is to approximate $\log P$ using a suitable machine learning model (e.g. our proposed step selection model), so that

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[7] `https://github.com/cifkao/moveformer`

[8] `https://pytorch.org/`

[9] `https://github.com/lucidrains/x-transformers`

[10] `https://github.com/rasterio/rasterio`

[11] `https://github.com/cifkao/gps2var`

Eq. (6) becomes *cross entropy* computed on trajectory *segments* of appropriate length. In our case:[12]

$$\begin{aligned} H_c &\approx -\frac{1}{N-1}\sum_{n=1}^{N-1}\log_K P\Big(y_{n+1}=1 \;\Big|\; \xi_{n-c+1\ldots n}, t_{n+1}, x_{n+1}^{(1\ldots K)}, z_{n+1}^{(1\ldots K)}\Big) \\ &= -\frac{1}{N-1}\sum_{n=1}^{N-1}\log_K P(y_{n+1}=1 \mid \psi_{n,c}), \end{aligned} \tag{7}$$

where we collapse all the conditioning variables to $\psi_{n,c}$ for brevity. For more fine-grained analysis, we may be interested not in the sequence-level cross entropy, but rather in the “pointwise” values, i.e. $-\log_K P(y_{n+1}=1 \mid \psi_{n,c})$.

More generally, we may alternatively choose to examine any metric that can be computed from the probabilities. We adopt the *relative entropy* (also known as the *Kullback-Leibler divergence*) of the prediction with the maximum context length $c_{\max}$ with respect to the one at context length c (as proposed by Cífka and Liutkus [174] in the context of causal language models for text):

$$\begin{aligned} &D_{\mathrm{KL}}\big[P(y_{n+1} \mid \psi_{n,c_{\max}}) \,\big\|\, P(y_{n+1} \mid \psi_{n,c})\big] = \\ &\qquad\qquad \sum_{i=1}^{K} P(y_{n+1}=i \mid \psi_{n,c_{\max}}) \log \frac{P(y_{n+1}=i \mid \psi_{n,c_{\max}})}{P(y_{n+1}=i \mid \psi_{n,c})}. \end{aligned} \tag{8}$$

Note that this metric does not depend on the ground truth location, but measures the amount of information gained by considering the maximal context instead of the limited one.

4.1.1 Relevant context length

We may expect that there would be a critical context length C after which the above metrics stop improving, as further extending the context does not result in significant information gain. Similarly to Riotte-Lambert et al. [11], we define the *relevant context length* C_m – for a given metric m – as the smallest context length for which the metric reaches its optimum, with a 5% tolerance for robustness to noise:

$$C_m = \min\left\{c\colon \frac{m(c) - \min_{c'} m(c')}{\max_{c'} m(c') - \min_{c'} m(c')} \le 0.05\right\}. \tag{9}$$

4.1.2 Efficient evaluation

We now discuss how to efficiently compute the probabilities needed to calculate the above metrics, following the procedure proposed for causal language models by Cífka and Liutkus [174]. We may collect all the probabilities in a tensor $\mathbf{P} \in \mathbb{R}^{N\times c_{\max}\times K}$ such that

$$\mathbf{P}_{n,c,i} = P(y_{n+1}=i \mid \psi_{n,c}). \tag{10}$$

Observe that by running the model on a segment of the trajectory corresponding to indices $n, \ldots, n+c_{\max}-1$ for a given n, we obtain all the values $\mathbf{P}_{n+c-1,c,*}$ for

---

[12] We use the number of candidates K as the base of the logarithm for consistency with Eq. (5) and noting that this amounts to a multiplicative constant $(1/\log K)$.

$c \in \{1, \ldots, c_{\max}\}$. We may also notice that $\mathbf{P}_{n,n,*} = \mathbf{P}_{n,n+1,*} = \ldots = \mathbf{P}_{n,c_{\max},*}$ for any $n < c_{\max}$. Hence, we can efficiently fill in the tensor $\mathbf{P}$ using N runs of the model on segments of length at most $c_{\max}$.

4.2 Candidate feature importance

While the parameters of step-selection models fitted by conditional logistic regressions or point-process models are directly interpretable [4], deep learning models are known as "black boxes" that require special techniques to be interpreted post-hoc. A simple but popular technique [175, 176] is based on testing the model on a dataset with the values of a given feature randomly permuted. While aware of the caveats related to using this technique with correlated features [177], we employ it here to demonstrate the possibility of interpretation, and leave more advanced techniques for future work.

Specifically, we study how individual *candidate features* (components of $\phi_n^{\text{cand},(i)}$) influence the selection of candidates. We pick a feature (or a group of features), and for every observation in the dataset, we randomly shuffle the feature's values among the K candidates (in contrast to Fisher et al. [176], who shuffle values across the entire dataset). The aim is to make the feature completely uninformative while maintaining its values plausible in the given context. We evaluate the model on both the permuted and the original dataset, and use the difference in performance as a measure of the importance of the selected feature.

5 Results

5.1 Validation

We evaluate the proposed model (here dubbed VarCtx) against variants to serve as baselines:

- FullCtx is a variant without the variable receptive field training (see Section 3.1.4);
- NoAtt is a model where all the attention layers are removed from the Transformer encoder, so that information is not allowed to flow between different positions in the sequence;
- NoEnc is a model where the Tranformer encoder is removed, i.e. we have $h_n = \phi_n^{\text{in}}$.

Note that the last two variants have a receptive field of 1 (i.e. only the features at position n are available for predicting the location at $n + 1$). To simulate this for VarCtx and FullCtx in a comparable way, we test these in a regime (denoted by +diag) where the attention matrices are restricted to an identity matrix, i.e. each position can only attend to itself.

After running each of the above models on the test set, we compute the following metrics:

- xent@16: cross entropy (Eq. (5)) computed with 16 candidates;
- xent@100: cross entropy computed with 100 candidates;

model	xent@16 ↓	xent@100 ↓	acc 1/16 ↑	acc 10/100 ↑
FullCtx	0.869	0.909	0.198	0.293
FullCtx+diag	0.990	0.998	0.102	0.157
VarCtx	**0.847**	**0.894**	**0.221**	**0.323**
VarCtx+diag	0.932	0.954	0.136	0.204
NoAtt	0.919	0.945	0.157	0.231
NoEnc	0.928	0.950	0.148	0.217

Table 2: Results for different variants of the model. FullCtx: trained on full trajectories (max. length 500); VarCtx: trained with variable receptive field; NoAtt: no attention layers; NoEnc: no encoder; diag: attention restricted to diagonal matrix during inference. Xent: cross entropy (lower is better), acc: accuracy (higher is better).

- acc 1/16: accuracy (i.e. how often the top scoring candidate is the ground truth) with 16 candidates,
- acc 10/100: top-10 accuracy (i.e. how often the ground truth is among the 10 top scoring candidates) with 100 candidates.

The results, averaged over all trajectories, are presented in Table 2. We note that the results are very consistent across all metrics, and we found all pairs of metrics to be strongly correlated (Pearson $\rho > 0.87$, computed over all models and trajectories).

Both FullCtx and VarCtx outperform the rest of the models, which have a receptive field length of 1. This is evidence that providing past movement as context is beneficial. Interestingly, VarCtx yields better results than FullCtx, possibly because the variable receptive field training scheme effectively makes the training data more diverse, alleviating overfitting.

We can also observe that the results of VarCtx+diag are closest to those of the models trained with minimum context (NoAtt, NoEnc). This suggests that the performance of VarCtx is not strongly degraded by limiting its receptive field at test time (unlike that of FullCtx), validating our variable receptive field training approach.

Finally, we noticed large performance differences between species. For the VarCtx model, we calculated the average cross entropy for each taxonomic order (see Table 3) and found that it tends to be lower (i.e. better) for orders with a higher number of observations in the training set (Pearson $\rho = -0.71$).

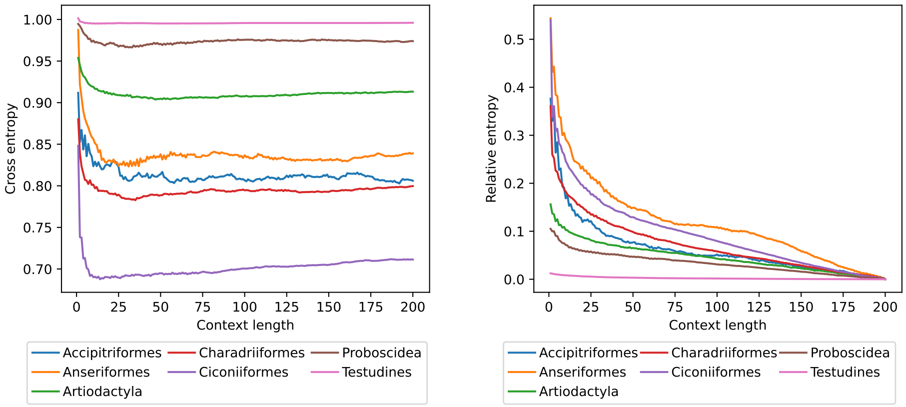
5.2 Context length analysis

In this section, we demonstrate the ability to use the VarCtx to study the dependence of the predictions on the length c of the available past context, as described in Section 4.1. We set $c_{\max} = 200$ and $K = 16$.

First, we display in Fig. 5 the average cross entropy and relative entropy as a function of context length and by taxonomic order, and in Fig. 5 examples for concrete observations, with the relevant context length C highlighted. We observe that the best predictions tend to be achieved around context lengths 10–50, which corresponds to 5–25 days.

class	order	xent@16	#train
Aves	Accipitriformes	0.815	58 994
	Anseriformes	0.827	64 008
	Cathartiformes	1.057	8653
	Charadriiformes	0.815	205 602
	Ciconiiformes	0.697	237 304
Mammalia	Artiodactyla	0.928	201 464
	Carnivora	0.986	12 282
	Proboscidea	0.980	24 870
Reptilia	Testudines	0.998	34 577

Table 3: VarCtx validation cross entropies by taxonomic order, along with numbers of observations in the training data.

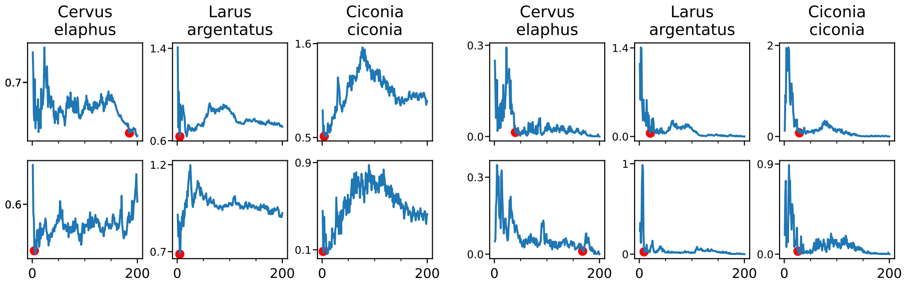


(a) Cross entropy (b) Relative entropy

Figure 4: Metric value averages by context length and taxonomic order, computed on the test set (only positions $n > c_{\max} = 200$).

Apart from the clear inter-species differences in cross entropy already noted in the previous section (Table 3), we also observe some differences in *relative* entropy, though less marked. For example, while *Ciconiiformes'* movements are substantially easier (in terms of cross entropy) for our model to predict than those of *Anseriformes*, both have a similar relative entropy profile, indicating that the amount of information contributed by each time scale is similar for both taxa. On the other hand, note that the flat relative entropy profile of *Testudines* simply reflects a failure of our model to accurately predict their movements at any time scale – as evidenced by the cross entropy values being close to 1 –, which is possibly due to an insufficient amount of reptile training data.

Fig. 6 shows the distribution of the relevant context length C for each taxon in the test set. There are apparent differences between taxa, but we also note the large variability *within* each taxon that could be of interest in itself.



(a) Cross entropy (b) Relative entropy

Figure 5: Examples of metric values (pointwise, i.e. for a single observation within a given trajectory) plotted as a function of context length. Top and bottom correspond to different (random) positions within the same trajectory. The red dot marks the relevant context length (where the metric reaches 5 % of its min-max range).

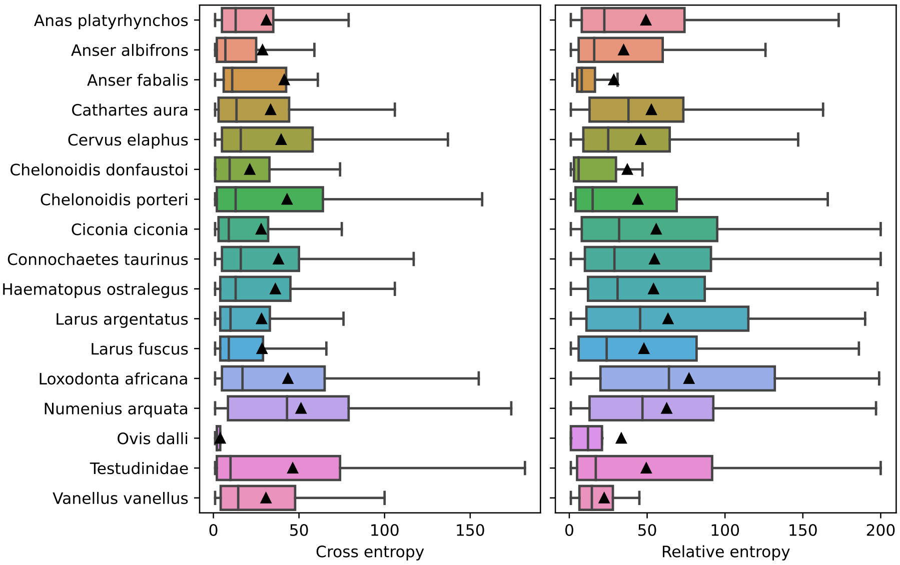


Figure 6: Relevant context length C by taxon, computed using cross entropy and relative entropy (pointwise values, as shown in Fig. 5), respectively. The black triangles indicate means.

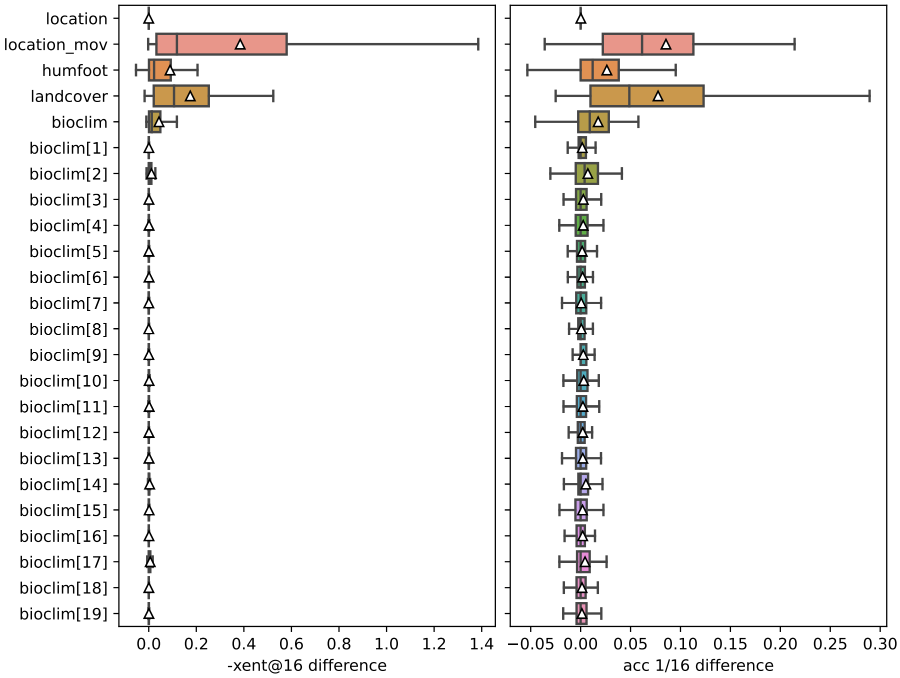


Figure 7: Candidate feature importances computed as differences between performance (measured using negative cross entropy and accuracy with 16 candidates) with and without permuted feature values. The plot shows the distribution over test trajectories. The features are, from top to bottom: location n-vector, movement vector, human footprint, land cover, and finally the 19 bioclimatic variables (BIO1 to BIO19), first as a group and then each individually.

5.3 Candidate feature importance

We present in Fig. 7 the results of the feature importance experiment. Vector features (location) are treated as groups; bioclimatic variables are tested both individually and as a group.

The most important features found by this method are movement vector and land cover, followed by human footprint. The bioclimatic variables appear to have relatively low impact, with the most important ones being BIO2 (mean diurnal range), BIO14 and BIO17 (both related to precipitation). Interestingly, global location (represented as n-vectors) seems to be the least important feature, possibly because it is difficult to exploit for candidate selection compared to the relative location information provided by the movement vectors.

Note that only *candidate* features $\phi_n^{\mathrm{cand},(i)}$ are tested here, and the results do not say anything about the *input* (past observation) features $\phi_{1\ldots n}^{\mathrm{in}}$. For example, global location, which we found to be unimportant as a candidate feature, may well turn out to be an important past context feature.

6 Discussion

In this work, we propose a new model to learn from animal trajectories. Inspired by the classical step-selection framework [2] and previous work on the quantification of uncertainty in movement predictions [11], we designed MoveFormer, a step-based model of movement that builds upon recent developments in deep learning, such as the Transformer architecture. This allowed us to meet our initial goal to endow the model with a unique ability to learn how past movements influence current and future ones. Although this is an important question in movement ecology, it has remained poorly addressed so far because classical step-selection functions or other movements models are unable to account for past information except in a very simplified way (e.g. by including a feature indicating whether or not the animal has previously visited a given site).

An important contribution of this work is also to generalize the suggestion of Riotte-Lambert et al. [11] to use conditional entropy calculated over visits to discrete sites as a way to measure movement uncertainty. Although attractive, the difficulty of discretizing trajectories to meaningful 'sites' has slowed down the application of this idea. Here, we extend it to locations acquired in continuous space and propose cross-entropy and relative entropy, estimated through the movement model, as a more general approach. This allows to estimate the *relevant context length* ('relevant order of dependency' in Riotte-Lambert et al. [11]), i.e. the amount of the past that significantly improves the predictions about further movements. We did so in this study, and to the best of our knowledge, our study therefore provides the first estimation of how much of the past one needs to know to improve predictions of animal movements.

Our results suggest that for most datasets, predictions are improved when integrating the information from about a few days to two or three weeks before the movement to be predicted. Why this is the case, and why these results are broadly consistent between species, with possibly significant within-species variability, remains to be investigated further as it was beyond the goal of this methodological work. We note that, possibly, these results are affected by our choice to alternate sampling at midnight and at noon and to limit the length of trajectories to 500 locations, restricting the receptive field of our model to about 250 days. This may have weakened or excluded the influence of migration, which commonly leads to seasonal back-and-forth movement patterns and that, when accounted for, could help improve predictions about future movements.

One obvious limitation of our approach is the data requirement. As with all deep learning approaches, learning is limited by the data available in the training set, and enough data should also be available for validation and test sets. The whole dataset we gathered here, despite being rather large ($>$ 1500 trajectories) compared to movement datasets currently analyzed in ecology, is likely close to the minimal size required to obtain a robust model and avoid severe overfitting issues. Currently, there are probably very few, if any, single-species datasets large enough to fit this model. For this reason, we aggregated data from numerous species; as a benefit, this allowed us to demonstrate that comparative analyses could be conducted with the model, for instance by comparing the distribution of relevant context lengths between species or higher-order taxa.

An important characteristic of the proposed approach is that the model not only accounts for past movements to predict new ones, but can also account for environmental predictors. First, this is crucial for realistic predictions, as the step-selection literature has well demonstrated that step selection by animals is critically linked to habitats to be traversed or reached. Second, this allows to evaluate the relative importance of predictors in improving predictions. Interestingly, we found that purely relative positional information (movement vectors) could be more important than environmental variables for future location prediction. We tentatively suggest that this result might be linked to the fact that most animals favor familiar places and by doing so restrict themselves to well-established home-ranges [178]. We however also found, without surprise, that among the environmental variables tested, land cover and human footprint significantly affected animal movements [179].

To summarize, in the present work, we provide a new, state-of-the art model to analyze and predict animal movement data. The novelty of the model lies in the fact that it leverages the power of deep learning approaches and can account for past movements in the predictions. However, we emphasize, and have shown above, that the model is not only a tool for prediction, but can also be used to test hypotheses about the intrinsic and extrinsic drivers of animal movements.

7 Acknowledgments

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We would like to thank all authors who made their data available through MoveBank under Creative Commons licenses (see Table 4 in the appendix for the list of datasets used in this work).

A Appendix

Table 4: The list of all Movebank datasets used in this work.

ID	Name and references	License
446579	MPIAB Lake Constance Mallards GPS [13]	CC BY
481458	Vultures Acopian Center USA GPS [14–17]	CC BY
1764627	Kruger African Buffalo, GPS tracking, South Africa [18–21]	CC0
2928116	Galapagos Tortoise Movement Ecology Programme [22–28]	CC BY
2988333	Navigation experiments in lesser black-backed gulls (data from Wikelski et al. 2015) [29, 30]	CC0
6770990	MPIAB PNIC hurricane frigate tracking [127]	CC BY
7002955	HUJ MPIAB White Stork GSM E-Obs [128]	CC BY
7431347	MPIAB Argos white stork tracking (1991-2018) [31]	CC BY
8019591	Dunn Ranch Bison Tracking Project [129]	CC BY
8849813	LifeTrack - Great Egrets [130]	CC0
8863543	HUJ MPIAB White Stork E-Obs [131]	CC BY
9493881	LifeTrack White Stork Uzbekistan [132]	CC BY
9651291	Egyptian vultures in the Middle East and East Africa [32–35]	CC BY
10157679	LifeTrack White Stork Tunisia [133]	CC BY
10204361	Pandion haliaetus Osprey - SouthEast Michigan [134]	CC0
10236270	LifeTrack White Stork Armenia [36–38]	CC BY
10449318	LifeTrack White Stork Loburg [135]	CC BY
10449535	LifeTrack White Stork Greece Evros Delta [36–38]	CC BY
10449698	HUJ MPIAB White Stork GSM 2013 [136]	CC BY
10596067	LifeTrack White Stork Moscow [36–38]	CC BY
10763606	LifeTrack White Stork Poland [37]	CC BY
14671003	Hooded Vulture Africa [137]	CC BY
16880941	Turkey vultures in North and South America (data from Dodge et al. 2014) [17, 39]	CC0
19411459	Movement ecology of the jaguar in the largest floodplain of the world, the Brazilian Pantanal [40–45]	CC0
20202974	e-Obs GPRS Himalayan Griffon - Bhutan-MPIAB [46–49]	CC BY
21231406	LifeTrack White Stork SW Germany [37, 38, 50, 51]	CC BY
24442409	LifeTrack White Stork Bavaria [38, 50, 52]	CC BY
69724677	FTZ Geese Wadden Sea [138]	CC0
74496970	MPIAB white stork lifetime tracking data (2013-2014) [36, 37, 53]	CC BY
92261778	LifeTrack Whooper Swan Latvia [139]	CC BY
133992043	Migration timing in white-fronted geese (data from Kölzsch et al. 2016) [54, 55]	CC BY
173641633	LifeTrack White Stork Vorarlberg [50, 56]	CC BY
178979729	Latham Alberta Wolves [57, 58]	CC BY-NC
178994931	Peters Hebblewhite Alberta-BC Moose [59]	CC BY
182746263	High-altitude flights of Himalayan vultures (data from Sherub et al. 2016) [47, 49]	CC0
190490326	Movement strategies of Galapagos tortoises (data from Bastille-Rousseau et al. 2016) [24, 26–28]	CC BY-NC
208413731	White-bearded wildebeest in Kenya [60]	CC BY
209824313	Hebblewhite Alberta-BC Wolves [61, 62]	CC BY
212096177	LifeTrack White Stork Oberschwaben [38, 50, 63]	CC BY
217784323	Vultures Acopian Center USA 2003-2016 [16, 17, 64]	CC BY
236953686	LifeTrack Ducks Lake Constance [140]	CC0
329155299	Canada geese (Branta canadensis) [141]	CC0
384868221	White-tailed Eagle Poland. [142]	CC BY-NC
475878514	Coyote Valley Bobcat Habitat Connectivity Study [143]	CC BY-NC

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Table 4: The list of all Movebank datasets used in this work. (Continued)

ID	**Name and references**	**License**
501787846	Aromas Hills Bobcat Habitat Connectivity Study [144]	CC BY-NC
505156776	Graugans Zugverhalten Neusiedler See [145]	CC BY-NC
560041066	Eastern flyway spring migration of adult white storks (data from Rotics et al. 2018) [65, 66]	CC BY
604806671	MH_WATERLAND - Western marsh harriers (Circus aeruginosus, Accipitridae) breeding near the Belgium-Netherlands border [67]	CC0
657674643	North Sea population tracks of greater white-fronted geese 2014-2017 (data from Kölzsch et al. 2019) [68, 69]	CC BY
657965212	Pannonic population tracks of greater white-fronted geese 2013-2017 (data from Kölzsch et al. 2019) [69, 70]	CC BY
672882373	Milvus_milvus_atlantismarcuard [146]	CC BY-NC
673728219	NPS Dall Sheep in Yukon-Charley Rivers National Preserve [147]	CC BY
736029750	ThermochronTracking Elephants Kruger 2007 [71, 72]	CC BY-NC
892924356	Milvus migrans [148]	CC0
897981076	Ya Ha Tinda elk project, Banff National Park, 2001-2020 (females) [61, 62, 73–78]	CC0
918219824	ECOPATH, Brown skua, Boulinier et al., Amsterdam Island [149]	CC BY-NC
922263102	H_GRONINGEN - Western marsh harriers (Circus aeruginosus, Accipitridae) breeding in Groningen (the Netherlands) [79]	CC0
933711994	Elk in southwestern Alberta [80–91]	CC BY
938783961	MH_ANTWERPEN - Western marsh harriers (Circus aeruginosus, Accipitridae) breeding near Antwerp (Belgium) [92]	CC0
985143423	LBBG_ZEEBRUGGE - Lesser black-backed gulls (Larus fuscus, Laridae) breeding at the southern North Sea coast (Belgium and the Netherlands) [93]	CC0
986040562	HG_OOSTENDE - Herring gulls (Larus argentatus, Laridae) breeding at the southern North Sea coast (Belgium) [94]	CC0
1030734949	Biotelemetry of Bewick's swans [95, 96]	CC0
1049685237	Greater white-fronted goose family migration flight [97, 98]	CC0
1071134107	Herring Gulls (Larus Argentatus); Ronconi; Brier Island, Canada [99, 100]	CC0
1077731101	Eurasian Curlews [ID_PROG 1083] [150]	CC BY-NC
1080341217	Herring Gulls (Larus Argentatus); Clark; Massachussets, United States [100, 101]	CC0
1080341737	Herring Gulls (Larus Argentatus); Ronconi; Sable Island, Canada [100, 102]	CC0
1087068449	Von der Decken's hornbill (Jetz Kenya) [103, 104]	CC0
1088836380	Carnivore movements near Black Rock Forest New York [151]	CC BY
1091848505	gullSpecies_USGS_ASC_argosGPS [105]	CC0
1092737859	GPS calibration data (global) [152]	CC BY
1099562810	O_WESTERSCHELDE - Eurasian oystercatchers (Haematopus ostralegus, Haematopodidae) breeding in East Flanders (Belgium) [106]	CC0
1123149708	Ivory gull N Greenland 2018/19 [153]	CC BY-NC
1208105916	Caspian Gulls - Poland [154]	CC0
1229945587	Common Crane 2020 (Lithuanian University of Educational Studies; LEU) [155]	CC0
1241071371	Arctic fox Bylot - GPS tracking [156]	CC0
1259686571	LBBG_JUVENILE - Juvenile lesser black-backed gulls (Larus fuscus, Laridae) hatched in Zeebrugge (Belgium) [107]	CC0
1260886163	Cheetah Pilanesberg National Park, South Africa, 2014-2015 [108, 109]	CC0
1266784970	Corvus corone [ID_PROG 883] [157]	CC BY-NC

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Table 4: The list of all Movebank datasets used in this work. (Continued)

ID	Name and references	License
1278021460	BOP_RODENT - Rodent specialized birds of prey (Circus, Asio, Buteo) in Flanders (Belgium) [110]	CC0
1285079529	Monitoring of Capra ibex (Bovidae) populations in the western alps (project ALCOTRA LEMED-IBEX) [158]	CC BY
1393954358	Cathartes aura MPIAB Cuba [159]	CC BY-NC
1395952585	FTZ: Migrating curlews (data from Schwemmer et al. 2021) [111, 112]	CC0
1410035327	HUJ MPIAB White Stork E-Obs (subset for Carlson et al. 2021) [113, 114]	CC0
1415844328	Moult migration of taiga bean geese to Novaya Zemlya [115, 116]	CC BY
1448377103	Wood stork (Mycteria americana) Southeastern US 2004-2019 [117, 118]	CC0
1448409403	Lapwing NFW Vanellus Vanellus [160]	CC BY-NC
1498452485	Variability of White Stork flight patterns prior to earthquakes [161]	CC0
1562253659	LifeTrack White Stork Sarralbe [ID_PROG 1093] [162]	CC0
1605798640	O_BALGZAND - Eurasian oystercatchers (Haematopus ostralegus, Haematopodidae) wintering on Balgzand (the Netherlands) [119]	CC0
1605799506	O_SCHIERMONNIKOOG - Eurasian oystercatchers (Haematopus ostralegus, Haematopodidae) breeding on Schiermonnikoog (the Netherlands) [120]	CC0
1605802367	O_VLIELAND - Eurasian oystercatchers (Haematopus ostralegus, Haematopodidae) breeding and wintering on Vlieland (the Netherlands) [121]	CC0
1605803389	O_AMELAND - Eurasian oystercatchers (Haematopus ostralegus, Haematopodidae) breeding on Ameland (the Netherlands) [122]	CC0
1606812667	Hawksbill/green turtles Chagos Archipelago Western Indian Ocean [123, 124]	CC0
1671751878	Tchad Redneck Ostrich [163]	CC BY-NC
1841261165	Eurasian wigeon (Mareca penelope) Netherlands Lithuania 2018-2019 [125, 126]	CC BY
1907973121	Lowland tapirs, Tapirus terrestris, in Southern Brazil [164]	CC BY-NC
1907974323	Vega gull (Larus vegae) - GPS - Russia South Korea Japan [165]	CC BY-NC

			#obs		
class	order	taxon	train	val	test
Aves	Accipitriformes	Cathartes aura	37609	2186	1703
		Circus aeruginosus	5537	—	—
		Circus cyaneus	540	—	—
		Circus pygargus	1088	—	—
		Gyps himalayensis	4047	736	312
		Haliaeetus albicilla	409	—	—
		Milvus milvus	323	—	—
		Necrosyrtes monachus	4337	951	126
		Neophron percnopterus	2138	—	—
		Pandion haliaetus	2966	181	—
	Anseriformes	Anas penelope	8297	—	—
		Anas platyrhynchos	22207	1970	1484
		Anser albifrons	18871	1122	558
		Anser anser	3549	—	—
		Anser fabalis	6258	—	244
		Anseriformes	1123	—	—
		Branta bernicla	1566	—	—
		Branta leucopsis	628	—	—
		Cygnus columbianus	602	—	—
		Cygnus cygnus	907	—	—
	Bucerotiformes	Tockus deckeni	4448	—	—
	Cathartiformes	Coragyps atratus	8653	—	312
	Charadriiformes	Haematopus ostralegus	44582	5439	3960
		Larus	196	—	—
		Larus argentatus	39655	8237	909
		Larus cachinnans	1021	—	—
		Larus fuscus	91380	8202	1534
		Larus glaucescens	293	—	—
		Larus smithsonianus	900	—	—
		Larus vegae	10018	—	—
		Numenius arquata	14896	—	1588
		Vanellus vanellus	2661	—	251
	Ciconiiformes	Ciconia ciconia	230170	5835	10402
		Mycteria americana	7134	—	—
	Gruiformes	Grus grus	189	—	—
	Passeriformes	Corvus corone	474	—	—
	Pelecaniformes	Ardea alba	1764	—	—
	Struthioniformes	Struthio camelus	221	—	—
	Suliformes	Fregata magnificens	521	—	—
Mammalia	Artiodactyla	Alces alces	3061	—	—
		Bison bison	130	—	—
		Cervus elaphus	158108	6648	3849
		Connochaetes taurinus	30036	755	4065
		Ovis dalli	9075	934	983
		Sus scrofa	556	—	—
		Syncerus caffer	498	—	—
	Carnivora	Acinonyx jubatus	239	—	—
		Canis lupus	4811	—	122
		Lynx	426	—	—
		Lynx rufus	4353	—	—
		Panthera onca	1873	—	—
		Vulpes lagopus	580	—	—
	Perissodactyla	Equus quagga	24873	709	—
	Proboscidea	Loxodonta africana	24870	5696	3539
Reptilia	Testudines	Chelonoidis	546	—	—
		Chelonoidis donfaustoi	9386	594	251
		Chelonoidis hoodensis	2251	—	—
		Chelonoidis porteri	12560	789	2283
		Eretmochelys imbricata	1286	—	—
		Testudinidae	8548	—	1859

Table 5: Number of observations of each taxon in each section of the dataset.

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