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Establishing the Integrated Science of Movement: bringing together concepts and methods from animal and human movement analysis

Supplementary information 1 – Similarities between animal and human movement concepts

This document describes similarities and differences between animal and human movement concepts and methods in more detail than the main text, with the goal to show potential pathways for interdisciplinary knowledge exchange.

How to read this document:

This document is closely integrated with the main manuscript. The main text provides a short overview of each of the tasks, while here we provide more details and references. Sections A-G correspond to sections 3.1. – 3.7. in the main document and sections H-L to sections 4.1. – 4.5. in the main text.

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I. Individual-based movement / Lagrangian analysis

A. Task L1: Space use

In this section we introduce concepts for space use in animal and human movement separately and attempt to identify similarities and linkages.

Two concepts that describe animal space use are home range and utilisation distribution. A home range is defined as a set of bounded areas used by the animal in the course of its normal activities (foraging, resting, taking care of the young) (Burt 1943, Powell and Mitchell 2012), while the utilisation distribution (UD) is a probability surface that describes the intensity of use of a particular location (Kie et al. 2010). The two concepts are methodologically linked, since a home range is calculated as a probability contour of the UD surface (Worton 1989), often 95%. More recently, ecologists have cautioned against equating the biological concept of the home range with the statistical method that is being used to calculate these areas from movement data (Fieberg and Börger 2012). While space use can be a result of different behavioural activities, such as foraging, resting, maximising fitness, finding partners, reproducing and surviving, describing the home range as only the space occupied during these activities is limiting. However, as occupied space is what could historically be most easily quantified from available data, it has become somewhat of a synonym with home range (Kie et al. 2010).

In human mobility, the equivalent measure of space use is an activity space, which is defined either as the spatial and potential extent of people's habitual movements (Patterson and Farber 2015), the movement space of an individual (Hurst 1969), or a locational choice of travellers (Rai et al. 2007). Activity spaces are represented by quantitative measures organised around key locations from daily routines, including home and work locations, as well as other significant places such as shops, parks and social meeting points (Schönfelder and Axhausen 2002) – these places are sometimes called activity points and, unlike in animal ecology, are often pre-identified from raw GPS points prior to quantification of activity spaces (see section 3.2. in the main document and section B here). Activity spaces play a role in understanding travel behaviours of groups and individuals, which makes them important for urban and transportation planning (Miranda-Moreno et al. 2012), mobility studies (Hirsch et al. 2014), as well as for understanding dynamics of neighbourhoods (Schönfelder and Axhausen 2002). In public health, activity space research links characteristics of the environment to health behaviours (Perchoux et al. 2019) - these methods represent a move from the more traditional focus on residence as the main context of exposure.

Methods for animal space use include geometric methods and kernel density estimators. A popular geometric method for home range is the Minimum Convex Polygon (MCP, Figure 2a in the main text), which fits a convex hull to a certain percentage (usually 95%) of observed movement points and was originally developed several decades ago for VHF data (Worton 1987) – in spite of (or perhaps because of) its simplicity, it is still frequently used (Laver and Kelly 2008). Other geometric methods include variations on MCP, such as a *n*-nearest neighbour convex hull (Getz and Wilmsers 2004) and characteristic hull polygons (Downs and Horner 2009). Kernel density estimators calculate the UD surface using a variety of kernels, from the standard 2D point pattern methods (Seaman and Powell 1996, Figure 2b in the main text), to non-parametric methods (Getz et al. 2007). Most of the space use methods in animal ecology are applied to raw locational data, that is GPS points, Argos locations or historically VHF observations.

Similarly, the most common activity space measures are ellipses, buffers, MCP, kernel density estimates (KDE) and network-based measures (Figure SI1_1). Ellipse-based methods (Figure SI1_1a) describe and visualise the geographical distribution of features by summarising dispersion and orientation of movement patterns (Rai et al. 2007). KDE methods (Figure SI1_1d) estimate kernel densities around activity points to demonstrate the intensity of these activities in space (Kwan 2000). Network-based measures calculate the shortest path between activity locations and create a buffer around this potential path in order to determine an activity space (Figure SI1_1b). These methods are often used together to study individual (Hirsch et al. 2014) and collective travel behaviour (Lee et al. 2016), accessibility to services (Xu, Belyi, Bojic et al. 2018), and environmental exposure in public health research (Perchoux et al. 2019, Wang, Kwan and Chai 2018).

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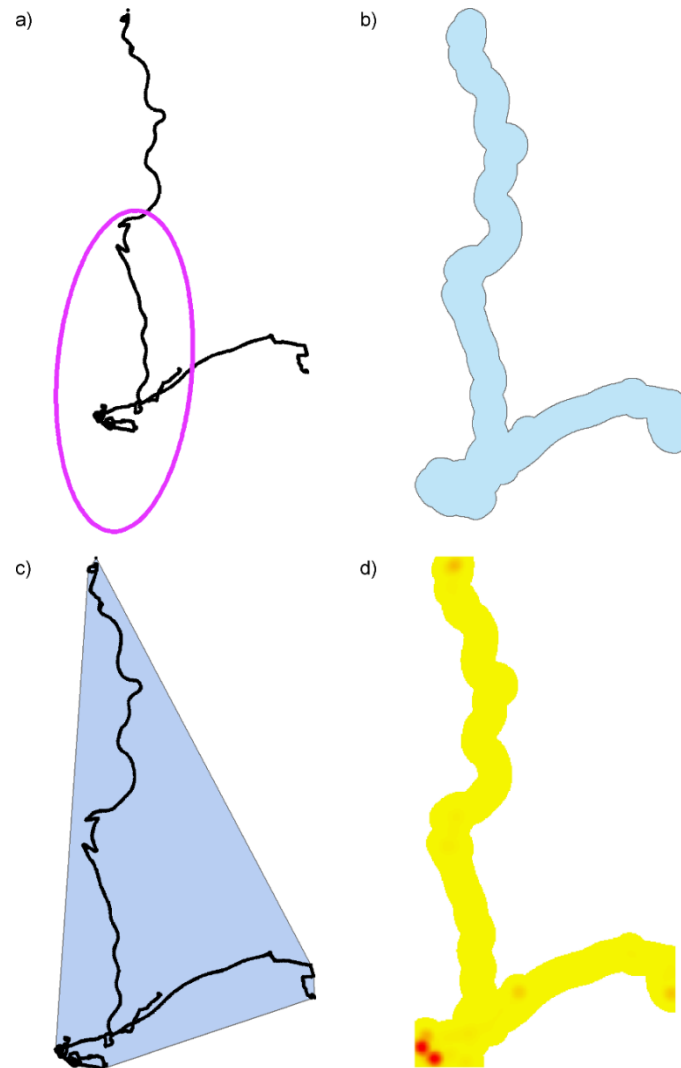


Figure S11_1. A set of activity spaces calculated for a participant from a GPS-based travel survey in Dunfermline, Scotland (Siła-Nowicka et al. 2016). Panel a) shows a standard deviation (STD) ellipse, b) is a road network buffer, c) a Minimum Convex Polygon and d) a Kernel Density surface, all calculated from the same data.

Until recently, neither geometric nor kernel methods in neither animal nor human movement research considered the temporal information in the data. This however is changing, with new geometric methods for space use based on time geography (Hägerstrand 1970), where (originally) human (but now increasingly also animal) movement is modelled using the principles of space-time cube (Hägerstrand 1970) and space-time prisms (Miller 1991, Miller 2005). In contrast with home range and activity space measures, which represent actual movement, time geography studies the accessibility space, that is, the only space within which the object could have moved given the physical constraints. For this, it represents the idea that space and time are inseparable in the form of a space-time cube where the two bottom dimensions show the two geographic dimensions and the third axis shows time. Movement trajectories are represented as polylines in this three-dimensional space and accessibility between observed locations is modelled using space-time prisms, which are volumes in the space-time cube within which a moving object had to move given its speed. A projection of a space-time prism on the geographic plane builds an ellipse, called a potential path area (PPA, Figure 2c in the main text). PPAs and space-time prisms are used in human mobility for quantification of accessible space (Patterson and Farber, 2015) as well as in ecology for estimation of physically possible animal home ranges (Long and Nelson 2012, 2015). Space-time prisms can also be combined with random walks and

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Brownian movement models, common in ecology, to develop a probabilistic measure of accessibility (Song and Miller 2014).

Other temporal methods include new kernel methods that use time to model the uncertainty in movement, such as Brownian bridges (Horne et al. 2007, Kranstauber et al. 2012), temporal extensions of non-parametric kernel methods (Lyons et al. 2013) and space-time densities (Demšar and Virrantaus 2010, Demšar et al. 2015).

Recent developments also take into account elevation, by developing new 3D kernels (Simpendorfer et al. 2012), extending Brownian bridges into four dimensions (Tracey et al. 2014a,b) and calculating Potential Path Volumes (Demšar and Long 2019, Figure 2d in the main text).

B. Task L2: Identification of movement behaviours

Behavioural patterns in movement data are identified through the process of segmentation, which decomposes movement data into sub-sections with similar characteristics (Buchin et al. 2010). Human mobility builds a semantic-trajectory model (Yan et al. 2013), which progresses from a raw trajectory (a sequence of spatio-temporal points) through a structured trajectory (segmented into stops and movement segments) to a fully semantic one (Figure 3 in the main text). In ecology, the phases of behavioural analysis are identical, without actually having an overall name for the methodology.

The first step in the human semantic model is a segmentation into parts with equal movement behaviour: stops and subtrajectories with a specific travel mode – driving, walking, etc. (Parent et al. 2013). In ecology, the former corresponds to sites of interest (Munden et al. 2018) and the latter to canonical activity modes (Getz and Saltz 2008). In human mobility, stops are called significant places, as they correspond to important locations in an individual's life (e.g. home, work, school) or places where repeated activities take place (e.g. sports facilities, grocery stores). Sometimes, Points Of Interest or Places of Interest are linked to segmented parts/stops, rather than directly to trajectory points (Yan et al. 2010, Siła-Nowicka et al. 2016). A typical segmentation looks at location persistence (termed site fidelity in ecology) and is based on temporal duration and frequency of visits (Benhamou and Riotte-Lambert 2012, Siła-Nowicka et al. 2016).

Trajectories can be segmented based on various physical parameters of movement (speed, heading, frequency and duration of visits, etc.) using rules-based methods (Stopher et al. 2008), fuzzy logic methods (Biljecki et al. 2013), or with spatial and spatio-temporal clustering (Chen et al. 2014, Gong et al. 2015). Travel modes are identified from the physical parameters of movement using various classification methods (Bolbol et al. 2012, Das and Winter 2018).

The final characteristic in the semantic model is the trip purpose which can be determined from integrated contextual data (see section 3.5. in the main document and section E here). This is often done using rule-based methods (Bohte et al. 2008), Bayesian methods (Meng et al. 2018) or by identifying the type of significant places (Liao 2003, Kang et al. 2013). In ecology, trip purpose corresponds to interpretation of behaviour, which is often done through direct observation or from video monitoring (Shamoun-Baranes et al. 2012) or using other sensors (e.g. posture identification through magnetometry, Williams et al. 2017).

Many behavioural studies in ecology segment not only GPS data, but also data from other co-located sensors, such as accelerometers or magnetometers (Nathan et al. 2012). For example, Williams et al. (2015) identify active (flapping) and passive (soaring, gliding) flight by segmenting tri-axial magnetometer data, while Chakravarty et al. (2019) segment accelerometer data to identify biomechanical behaviours of meerkats. Behavioural studies in public health use a combination of GPS and accelerometer to estimate levels of physical activity and link them to environmental exposure (Allahbakhshi et al. 2020).

A frequent problem in ecology is that movement behaviours occur at different temporal scales, which are not recognisable a-priori (Nathan et al. 2008). Solutions to this problem are inspired by signal analysis and use frequency decomposition algorithms to segment the time series of movement parameters, such as speed or acceleration (Ahearn and Dodge 2017, Soleymani et al. 2017).

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C. Task L3: Interaction of moving objects

The idea that individual movement is impacted by other moving individuals is termed dynamic interaction (Long and Nelson, 2013), but several other terms have also been suggested, most notably space-time interaction (or association) (Kenward et al. 1993), bundling (Hägerstrand 1970), and social interaction (Farber et al. 2013). Numerous methods have been developed to characterize dynamic interactions that may emerge from movement processes, for example methods that focus on contacts between individuals are commonly used to study the potential for disease transmission in wildlife (Böhm et al. 2009) and among humans (Breakwell et al. 2015). Currently of high importance, analysis of real-time dynamic interaction through contact tracing apps is an essential tool for managing the ongoing COVID-19 pandemic (Oliver et al. 2020a,b). Dynamic interaction methods have been applied in both human and wildlife examples extensively, but also in other areas of research, such as sports analytics (Bourbousson et al. 2010), and human-computer interaction studies (Demšar and Çöltekin, 2017).

Methods for studying dynamic interactions can be categorized as either pair-wise, focusing only on the interaction between two individuals (Long et al. 2014, Miller 2015) or group-based, studying simultaneous interactions between more than two individuals (Benkert et al. 2008, Laube et al. 2005). Methods used to study interactions may be point-based, path-based, or area-based, depending upon how they treat the spatial-temporal geometry of the movement data. These methods all suffer from similar issues, such as choosing spatial and temporal thresholds to define interactions and how these choices influence resulting pattern of interaction captured in the data (Long 2015, Long et al. 2014). One of the biggest challenges in the study of dynamic interactions is that it is extremely difficult to capture what represents a significant or unexpected level of interaction, over and above what might be expected (Long 2015, Miller 2015).

Interaction of moving objects is also popular in computational geometry which designs efficient algorithms for solving geometric problems. There is often no particular human or animal application in these studies (Gudmundsson and Van Kreveld 2006), as they are normally done at a highly abstracted level with trajectories being considered conceptual objects. Occasionally there are dedicated implementations for a specific purpose, such as for geometric analysis of movement in team sports (Gudmundsson and Horton 2017). Unlike many more statistically oriented methods for dynamic interaction in ecology and human geography, computational geometry quantifies interaction through geometric similarity amongst individual moving trajectories. There are methods to identify flocks (i.e. sets of objects that move in close proximity to each other, Benkert et al. 2008), groups (Van Kreveld et al. 2018), single files (objects that move one after another, Buchin et al. 2010a) and methods that quantify geometric distance between two trajectories in space and time (e.g. the so-called Fréchet distance, Buchin et al. 2019).

Similarity of trajectories has also been a popular problem in the data mining community in computer science. There are numerous algorithms that cluster trajectories into those that represent similar movement (Nanni and Pedreschi 2006) or those that combine visual and analytical methods to identify similar traces (Rinzivillo et al. 2008, Andrienko et al. 2017b). A popular application area is sports analytics, in particular group sports where knowledge about simultaneous and interactive movement of several players is crucial (Andrienko et al. 2019).

New technology specifically targeting interactive behaviour uses sensors that can detect when individuals are within a pre-specified distance of another. In wildlife systems these devices are called proximity loggers and are now used frequently in wildlife tracking studies to study contacts between con- (Ji et al. 2005) and cross- specific (Böhm et al. 2009). These sensors can now be integrated into GPS tracking loggers to provide simultaneous location tracking and proximity data (Ossi et al. 2016). Bluetooth and wireless technologies, primarily through modern mobile phones, can be used in a similar way to detect contact networks in human systems (Natarajan et al. 2007), real-time proximity of individuals for epidemiological contact tracing (Cho et al. 2020) or behaviour of crowds at large events (Versichele et al. 2012a, b). As the data from all these proximity sensors is also often used for a population level analysis rather than for individual movement, see also section 4.4. in the main document and section K here.

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D. Task L4: Collective behaviour

Collective motion is the synchronised movement of a group of individuals, where the group creates a structure that moves as one body and where at the same time individuals in the group do not have a complete picture of their position in the overall structure (Sumpter 2006). The central principle of collective motion is the process of self-organisation that emerges from local interactions of individuals with their nearest neighbours, both in human (Warren 2018) and animal collective behaviour (del Mar Delgado et al. 2018). Examples are found in both animal and human movement at different spatial and temporal scales. A typical and well-studied example in ecology is collective motion of starlings in a murmuration (Stamps et al. 2019). In human mobility the study of collective behaviour is known as crowd behaviour, with a particular focus on pedestrian behaviour in large crowds, which may require evacuation or where panic may occur (Helbing et al. 2000), e.g. the Hajj (Johansson et al. 2012) or the Notting Hill Carnival (Batty et al. 2003).

Collective motion was for a long time a difficult phenomenon to study, due to the challenge of simultaneously monitoring several individuals. However, recent technological developments provide a variety of new ways to observe how groups and individuals in groups move. These include identification of group and individual behaviours from imagery or videos using computer vision (Hughey et al. 2018,) and artificial intelligence methods (Graving et al. 2019). Animal-mounted cameras or sound recorders provide information on passive and active information flows that reach beyond the nearest individuals, such as vocalisations or gestures. Proximity sensors provide information on social networks and interactions in the group: there is growing evidence that both animal collective behaviour (Couzin 2018) and motion of human crowds (Warren 2018) are affected by social cues.

As data on collective motion differ, so do methods. Collective navigation of migratory animals is explored using agent-based models (ABMs, see section 3.6. in the main document and section F here for more), where agents' behaviour is determined both by their own abilities, sensory information, local landscape information and through influence of nearby neighbours and social learning (Berdahl et al. 2017). Similarly, pedestrian crowd behaviour in human mobility is investigated through crowd simulation with agent-based models (O'Sullivan and Haklay 2000), cellular automata (Burstedde et al. 2001), fluid dynamic models (Hughes 2003) or models based on high-frequency crowdsourced locational data, obtained through apps (Blanke et al. 2014). Other methods in ecology include geometric measures to investigate leading/following in migration (Flack et al. 2018), and spatio-temporal video analysis (Stamps et al. 2019). For humans, video surveillance and detection of individual motion from airborne video data is used to build crowd simulation models (Almer et al. 2016). Irfan and Tokarchuk (2016) provide a review of visual (video) and non-visual (sensor-based, mostly mobile phone) methods for analysis of crowd behaviour.

Crowd dynamics is also frequently modelled using Eulerian data, such as data from Bluetooth/wireless sensors, proximity sensors and CCTV camera data, more on this in section 4.4. in the main document and section K here.

E. Task L5: How does environment affect movement decisions?

Ecologists include environmental data into statistical models of movement in the form of covariates or factors. These include products from satellite remote sensing (Pettorelli et al. 2014), land cover data (De Groeve et al. 2015) or meteorological data (Safi et al. 2013). Among satellite products, the Normalised Difference Vegetation Index (NDVI) is popular, as it links the seasonality of movement with the greenness of the landscape, and allows to explore the “surfing the green wave” effect in migration of large land mammals (Bischof et al. 2013) and of birds (Shariatnajaabadi et al. 2014). Most of the studies use only a single satellite source, thereby ignoring issues of integration of data across temporal and spatial scales, however, recently multi-source approaches have been proposed that aggregate environmental data from several satellite sources or across spatio-temporal scales (Berman et al. 2019).

The process of attaching values of environmental data to each trajectory point is called trajectory annotation. One of popular trajectory annotation systems is Env-DATA (Dodge et al. 2013), which is housed by the largest repository of animal tracking data, *Movebank.org* (Wikelski et al. 2020). Env-

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DATA facilitates the integration of trajectory data with over one hundred environmental variables derived from satellite products stemming from NASA, ESA and other agencies (Figure SII_2). In GIScience, a term for the combination of trajectory annotation and data mining of annotated data is Context-Aware Movement Analysis (CAMA, Purves et al. 2014). Most GIScience studies use CAMA in the human mobility context. For example, Brum-Bastos et al. (2018) and Horanont et al. (2013) evaluate the effect of meteorological conditions on human movement (Figure SII_3).

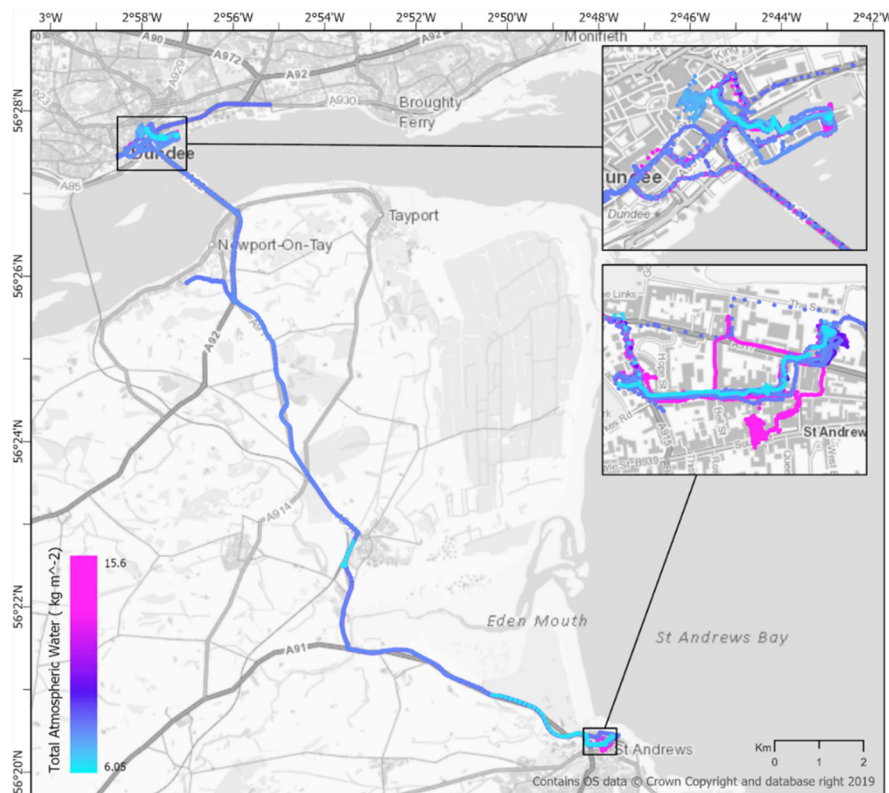


Figure SII_2. Trajectory annotation with Env-DATA. Figure shows an annotated GPS trajectory of a commuter who travels on a bus between Dundee and St Andrews in eastern Scotland. GPS data were collected over four days with a temporal resolution of 5Hz. Trajectory was annotated with the total atmospheric water variable (clearly identifying the typically *dreich* Scottish weather conditions during the four days of data collection), which came from the European Centre for Medium-Range Weather Forecasts (ECMWF) and was automatically linked to the GPS points through the Env-DATA portal using bilinear interpolation.

In computer science there is a further analogous terminology for integration of trajectories and contextual data: the process of annotating trajectories is called semantic enrichment (Parent et al. 2013). Annotations can be attached either to the entire trajectory or its subset, to create a so-called semantic trajectory (Alvares et al. 2007, see also section 3.2. in the main document and section B here). These are then used as input to various further analyses, often employing trajectory data mining (Pelekis and Theodoridis 2014) or fitting movement models, such as for example spatial interaction models (Yue et al. 2012, for more on these see section 4.3. in the main document and section J here).

A related problem commonly encountered in geography and transportation is called map-matching (Marchal et al. 2005) and links trajectories to road network data to identify street segments used by individuals. This appears in various contexts, from reconstruction of traffic restrictions (Efentakis et al. 2017) to real-time analysis of drivers' behaviour (Houbraken et al. 2018). It is sometimes inspired by collective animal movement (Gong et al. 2018).

Trajectory annotation, context-aware movement analysis, semantic enrichment and map-matching are all examples of spatio-temporal data fusion, another term that refers to the same process of linking

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movement and environmental data. These additional data vary: in computer science and transportation they are typically other objects (e.g. points of interest (POIs), places of interest, road networks, etc., Yan et al. 2013, dos Santos Mello et al. 2019), and in ecology they are typically environmental raster data (Pettorelli et al. 2014), as discussed above.

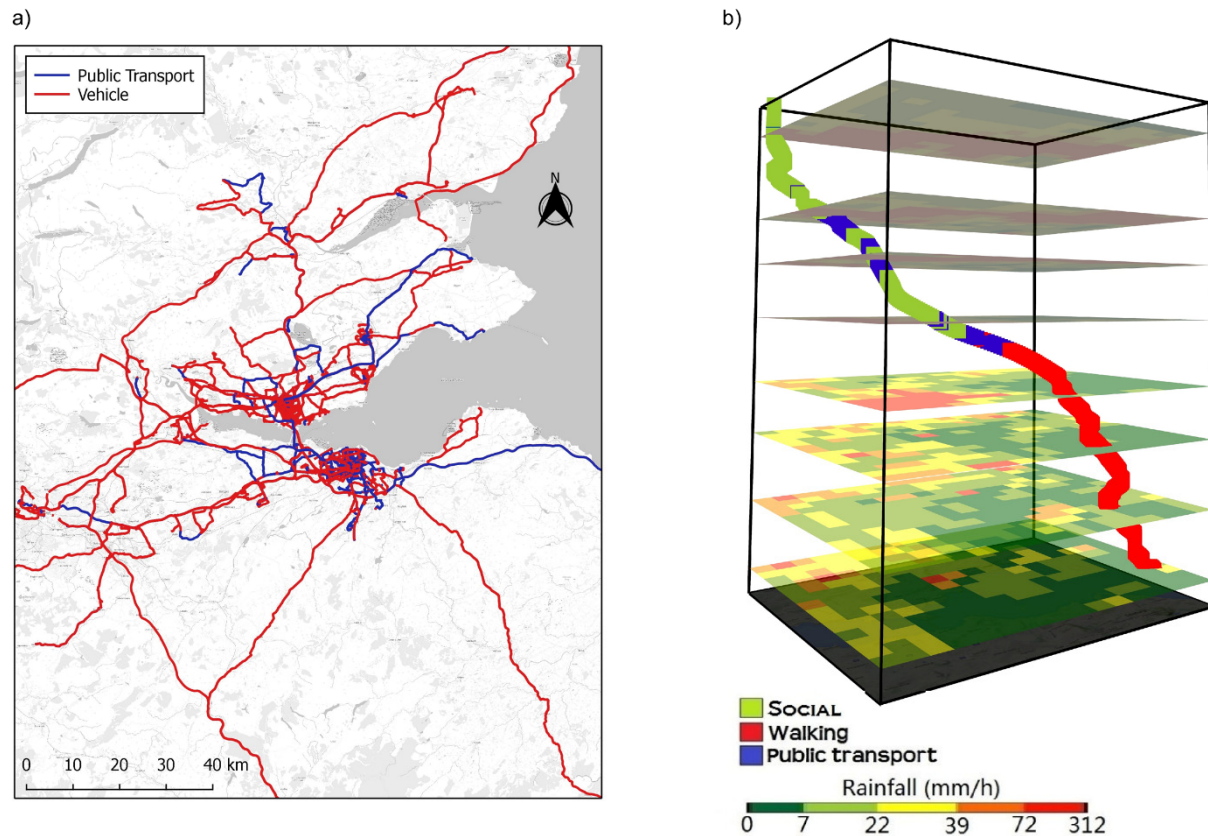


Figure SI1_3. Annotating trajectories of commuters with rainfall radar data for CAMA. Panel a) shows trajectories of commuters from Dunfermline, a town in the Scottish county of Fife. Commuters were tracked for 2 weeks and their trajectories segmented into stops and travel modes. In panel b), one of these trajectories is shown in a space-time cube as a polyline segmented into travel modes, along with raster layers of rainfall radar data, in preparation for annotation. After Brum-Bastos et al. 2018.

Data fusion of contextual and movement data is fundamentally affected by the different spatial and temporal scales of the data to be fused (Pettorelli et al. 2014). In ecology, GPS trajectories of a moving animal can be sampled at very high temporal scales (1Hz), while satellite remote sensors can provide relevant environmental data with either high spatial or high temporal resolution, but not both (e.g. satellites with sensors with high spatial resolution (0.5m-30m) have temporal resolutions from several days up to several months, while those with low spatial resolution (e.g. 250m-1km) cover the same area daily). This means that linking satellite remote sensing data with GPS trajectories introduces a problem of selecting the correct scale and/or creating “missing” and potentially incorrect data at a high temporal scale (usually through some kind of interpolation), that may not correspond to the actual environmental situation (Brum-Bastos et al. 2018). In public health, a similar problem is described through two concepts, the Uncertain Geographic Context Problem (UGCoP, Kwan 2012) and the Neighbourhood Effect Averaging Problem (NEAP, Kwan 2018). UGCoP occurs when contextual data come as areal data and states that the uncertainty in these data arises from variations of delineations of the areas in which the data are collected (this is similar to the well-known Modifiable Areal Unit Problem MAUP in geography, but related to context, not to the main data). This is similar to the scale mismatch in linking trajectories and satellite data in ecology. The NEAP occurs when mobility-related phenomena, such as exposure to air pollution, are modelled based on residence location, thus ignoring the levels of

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exposure during the day. The ecological equivalent of time spent out of the primary residence is central-place foraging (Stephens et al. 2007), a behaviour where the animal makes repeated back-and-forth foraging trips from a central location (e.g. to bring food to the young in the nest). This is addressed either by only performing the analysis on the data from outside the central location (for an example see Demšar et al. 2015) or by subtracting the null model of distance use that takes into consideration declining resource use with distance (Rosenberg and McKelvey 1999) - in the same way physics removes the central null model (Expert et al. 2011, see section 4.2. in the main document and section I here).

Once movement and environmental data are linked, researchers can explore how movement decisions are influenced by the state of the local environment. In ecology, the most common method for studying how individuals make movement decisions in relation to the environment is step-selection analysis (Fortin et al. 2005, Thurfjell et al. 2014). Here observed movement data for every step (typically defined as a pair of consecutive GPS points) are compared to a sample of random available steps. Environmental covariates are included for each used and random step and are then analysed using a regression model to extract covariates relevant for understanding movement-environment relationships (Thurfjell et al. 2014). Extensions of step selection analyses include individual effects (Duchesne et al. 2010) and movement-specific covariates (Avgar et al. 2016). Inferring movement environment relationships can occur across a range of movement scales (Holloway 2019) and step selection analysis is employed because it captures local movement decisions, which are associated with the resolution of the tracking data. Coarser analysis can be used to study route choices over longer periods, for example, Technitis et al. (2015) demonstrate a method for comparing real to randomly generated movement paths between known origin and destination pairs, used to compare migratory routes.

In human mobility, route choice models are used to understand the characteristics of travel decisions. Route choice models compare a chosen route with a set of alternative routes. These types of models are congruent with other movement decision models, such as mode-choice and destination choice models (Prato 2009). These are derived from utility theory, which states that a traveler maximizes the utility by choosing a route from a set of available routes, often referred to as Random Utility Maximizing (RUM) models. Route choice models are evaluated using logistic regression (Ben-Akiva and Bierlaire 1999), and random forest models (Tribby et al. 2016), along with other modifications based on existing travel theory (Prashker and Bekhor 2000).

Similarities between movement-decision models used in human and wildlife studies go beyond the statistical machinery used for inference. In both cases, the goal is to compare observed movement data to potential opportunities to make inferences about how environmental and contextual features influence movement decisions (Figure 4 in main text). In the wildlife case this is done by comparing observed movement steps to random steps (Figure 4a). In the human mobility case models require a similar definition of the route choice set, which defines the potential routes connecting an origin and destination across a spatial network (Figure 4b). The fundamental difference is the scale of analysis and the type of underlying geometry (Holloway 2019). In wildlife studies this analysis is conducted at the scale of the 'step' defined by two consecutive locations, which is along a straight line and has a specific length and direction (Thurfjell et al. 2014), whereas in human mobility studies this is typically defined at the 'trip' level, defined as travel between two activities and can consist of several turning steps (Prato and Bekhor 2007) – a trip is often derived from semantic trajectories (see section 3.2. in the main document and section B here). See (Richard and Armstrong 2010) for a similar example in the wildlife context.

F. Task L6: Models and prediction of movement

Movement models are used to simulate individual patterns or collective population flows (for the latter see section 4.3. in the main document and section J here). These models are created to explore and predict movement, to reveal hidden spatio-temporal regularities and to better understand movement behaviour under various conditions (Hess et al. 2015). This has applications in movement ecology, location-based services, urban planning, epidemic control and transportation. In ecology, models are

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used to explain behaviour (McClintock et al. 2012), as well as make inferences about the relationships between movement, behaviour, and associated covariates (Hooten et al. 2017). In human mobility, an added dimension is to not only analyse movement, but also predict social interactions (Barbosa et al. 2018).

A popular class of movement models in both animal and human movement research are random walks. Random walks simulate movement trajectories by modelling the step length (the consecutive distance between two recorded locations) and the turning angle (the relative change in direction of movement) at each moment in time (Codling et al. 2008, Turchin 1998). Ecologists utilize both discrete-time (Langrock et al. 2012) and continuous-time random walks (Harris and Blackwell 2013). Individual human mobility is often modelled using a class of continuous-time random walks, where displacements (step lengths) and wait time between individual steps are drawn from a truncated power-law distribution (Gonzalez et al. 2008). Similarly, attempts have been made to empirically show that some forms of animal movement follow a random walk with truncated power law distribution for step length – termed a Lévy flight (Viswanathan et al. 1996, 2000), but see Edwards et al. (2007) for some conflicting findings on this topic.

One popular modification of random walks in ecology is the inclusion of directional persistence (often modelled as autocorrelation in turning angle) to create correlated random walks (Kareiva and Shigesada 1983). Another is to include a bias term in movement direction (termed a biased random walk), for example movement may be biased to the centre of the home range (Moorcroft et al. 2006). In ecology, these models require empirical data on animal's movement physiology as a biological base of the simulation, which helps derive animals' turning angle, step length and speed (Tang and Bennett, 2010). Random walks for human mobility are often extended by incorporating exploratory behaviour and preferential returns to known locations (Song et al. 2010a), or by favouring recently visited places (Barbosa et al. 2015).

A more general class of methods are Agent-Based Models (ABM), which model movement responses of an individual agent at every point in time and can incorporate interactions with their environment and with other individuals (O'Sullivan and Perry, 2013). In human mobility, ABMs are used to model human navigational strategies (Giannopoulos et al. 2014) and wayfinding tasks (Wiener et al. 2015), for transportation (Martinez et al. 2015), for pedestrian crowds (Vemula et al. 2017) and for movement in 3D using information from multiple sensors (Barriuso et al. 2017). In ecology, movement related ABMs are used in a wide range of animal species ranging from insects to fish, birds, insects, large herbivores, carnivores and omnivores (Bennett and Tang 2006, Tang and Bennett, 2010, Oloo et al. 2018). They have been used to study individual behaviour (e.g. habitat selection, foraging), group related behaviour (e.g. dispersal, migration) and interactions between different species of animals (e.g. predator prey interactions), as well as proximate movement patterns and the effect of the environment (navigation, wind drift) (McLane et al. 2011, DeAngelis and Grimm, 2014).

Movement models in both ecology and human mobility studies offer significant potential for prediction. In both cases, prediction can be thought of as being either of two cases: i) interpolation – i.e., predicting missing data, or movement between existing location points, and ii) extrapolation – using a specified model to predict future or past movement behaviour, simulate data, or test different scenarios.

Interpolation is a frequent choice for prediction in both animal and human movement research and is often done using similar methods. For example, Technitis et al. (2015) build a random walk model for interpolating avian migration data, while Song et al. (2016) design similar random walk models to interpolate mobility patterns in transportation networks.

Prediction via extrapolation is particularly popular in physics and computer science, which frequently take a view that (human) movement is regular and therefore predictable (Song et al. 2010b). This enables creation of advanced forecasting algorithms, which can be divided into three main groups: Markov-based methods, time-series methods and machine learning methods (Zeng et al. 2017, Kulkarni et al. 2019), used across animal and human movement

Markov-based methods predict individual's location by defining a set of states, each describing a specific movement behaviour and then estimating transition probabilities from a historical trajectory using information about last n -states (Ashbrook and Starner 2003). Hidden-Markov Models (HMMs) are used to make inferences about how movement patterns (observed data) relate to underlying behavioural states (hidden layers) (Cielniak et al. 2003). These models are increasingly commonplace

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in ecology, where they are used to infer behaviour and explore how presence of other individuals or environmental covariates affect animal movement (Langrock et al. 2012, Michelot et al. 2016, Leos-Barajas et al. 2017). In human mobility, Markov models were popular in the early 2000s (Ashbrook and Starner 2003, Cielniak et al. 2003), however, some recent physics studies suggest that human movement may have a non-Markovian nature (Zhao et al. 2015) and argue that these models are therefore not suitable to predict human movement.

Time-series models were adapted from the classical approach to time-series forecasting. They include linear and nonlinear multivariate predictors, that enables addition of external data (De Domenico et al. 2013). In animal movement, time series models are frequently used on both Lagrangian (Gurarie et al. 2009) and Eulerian data (see section 4.3. in the main document and section J here).

Unlike ecology and human geography, where the focus of modelling is primarily to explain a specific phenomenon, computer science and physics evaluate models based on how accurate their predictions are compared to some known outcome. This type of analysis has become particularly common in for human mobility in recent years, when the increase in computational power and data availability has lead to high popularity of machine learning (ML) and artificial intelligence (AI) methods (Wang, Dong, Cheng et al. 2019). These methods are often some kind of new types of neural networks, such as deep or recurrent neural networks (Kulkarni et al. 2019), which often incorporate additional contextual information to further improve accuracy (Cuttone et al. 2018). We however note that using AI methods for modelling human mobility is not new and has been around since 1990s (Black 1995).

Using ML/AI methods to predict movement is not useful unless informed with domain knowledge. ML/AI models are excellent for specific narrow tasks, which require fast analysis of large amounts of data – for example, to predict properties of individual movement from videos of grazing animals (Graving et al. 2019) or of pedestrians (Xu et al. 2018). Unfortunately, many current ML/AI studies for movement, in particular in methodological disciplines, do not attempt to solve a specific problem, but simply apply these new methods on an old data set (often a random set of twitter trajectories or similar social media data) and overclaim significant results while presenting a marginal improvement in accuracy, none of which seems to be very useful or beneficial for movement research. Further, ML/AI models are computationally demanding and therefore hold a very significant environmental cost (for example, Strubell et al. 2019 report that training a not particularly big and relatively common deep learning network created as much carbon emissions as two average Americans generate during their entire lifetime). A further drawback of ML/AI models is that they can only learn from past data and therefore the exploratory nature of movement is never predicted. They also replicate biases in the data, which may disadvantage specific individuals or groups (Van Noorden 2020) – we note that this is a problem for human mobility rather than animal movement research (where ML/AI methods are also not as ubiquitously and blindly used). These issues are currently being brought to light and ML/AI researchers are being encouraged to both forge interdisciplinary connections to develop meaningful models and to consider ethical issues as a pre-condition for their research (Lo Piano 2020).

G. Task L7: Visualising individual movement

Lagrangian movement data are usually geometrically simple objects (e.g. GPS or other trajectories), but where each trajectory point can contain many attributes. Trajectories are often long, densely temporally sampled and overlapping. Visualising such data is therefore complicated and full of problems, such as overprinting and occlusion (Demšar et al. 2019) - see for example figures SI1_2 and SI1_3, where vehicle trajectories follow the underlying road network and where it is impossible to tell how many trajectories have actually passed over a specific road segment.

The majority of the movement visualisation literature provides methods for GPS trajectories. Very common are the so-called “spaghetti maps”, which simply show trajectories on a geographic map. These are frequently used in ecology, sometimes shown just as lines and at other times using some attribute to show properties of individuals or environmental values at certain trajectory locations (see Katzner et al. 2012, Mattern et al. 2018 for examples). Spaghetti maps and their variations in space-time cube are also common in transportation and computer science (Andrienko et al. 2017b, Chen et al. 2015).

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Maps displaying space use are also popular, in particular kernel density maps or heatmaps (as they are called in computer science), see for example Mattern et al. (2018) for graphically well-designed KDE maps. In animal ecology, recent space use visualisations add time (Demšar et al. 2015a) and environmental information (Buchin et al. 2015) to kernel density maps or visualise space use in real 3D (Tracey et al. 2014a, b). An unusual visualisation of 3D space use aggregates data points into hexagonal prisms (Ferrarini et al. 2018).

Temporal visualisations for GPS trajectories support identification of specific places and temporal profiles of movement – some animal movement examples include Kölzsch et al. (2013), Slingsby and Van Loon (2016, 2017a,b), while Bach et al. (2017) provide a review of and a framework for temporal visualisations in a space-time cube that also includes representations of human mobility.

Visual analytics systems for movement consist of interactively linked views and provide a possibility to explore different aspects of the same data. DynamoVis (Xavier and Dodge 2014, Dodge et al. 2018) which links multi-dimensional trajectory maps with environmental and temporal visualisations and provides animation possibilities. A second one is a system by Konzack et al. (2018), which provides two aggregations of migration trajectories: a generalisation into OD flows between identified stopover sites (Figure 5 in main text, top left panel) and a kernel density map of trajectories with a possibility to visualise individual trajectories (Figure 5 in main text, top right panel). Somewhat differently, Konzack et al. (2017) provide a visual analytics system for exploration of dynamic interaction. . There are only a few visual systems aimed at Lagrangian movement data from sensors other than GPS and most of these come from movement ecology. An example is an m-sphere for magnetometry data that allows the ecologist to visually analyse posture patterns (Williams et al. 2017).

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II. Place-based movement/ Eulerian analysis

H. Task E1: Space use

Space use analysis using Eulerian data, such as origin-destination flows, are common in ecology, but not in human mobility. Flow data are particularly important to study movement of marine animals, where tags using GPS localisation cannot be used and where most of the information on animal movement comes from passive acoustic telemetry (Kessel et al. 2014).

The simplest way to investigate space use from passive acoustic array data is to treat observations on an acoustic trajectory as a point pattern data set and calculate the mean centre of locations at specific moments in time (Simpendorfer et al. 2002). This is called the Centre of Activity (COA) analysis (not to be confused with activity space in Lagrangian human mobility, section A) (Heupel et al. 2018). Acoustic data further often use Lagrangian type space use methods, such as kernel density for utilisation distribution from acoustic trajectories (Papastamatiou et al. 2017) or from COA trajectories (Heupel et al. 2018) – this mirrors the semantic trajectory model from human Lagrangian analysis (section B, Figure 3 in main text).

Acoustic data provide a reliable measurement of depth, and therefore analysis of 3D space use is more widespread in aquatic context than for terrestrial or aerial animals (Simpendorfer et al. 2012, Heupel et al. 2018). Studies also include environmental data, for example bathymetry to avoid modelling pitfalls such as animals swimming through islands (Aspillaga et al. 2019). Newer studies combine passive long-term acoustic data (collected over months to years) with short-term sensor data (from tags with accelerometers deployed over a few days) to create a simultaneous representation of space use and activity levels (Figure 6 in main text) (Papastamatiou et al. 2018).

Eulerian methods for space use are rare in human mobility, although there are a few individual studies with kernel density estimators for flow data: for example, Rae (2009) uses KDEs to show density of human migration along migration flows. While creating a KDE may make sense in the context of tracking marine animals (e.g. a shark can swim directly between two given locations and uses the space in-between), in the context of human migration it implies a spurious pattern of direct paths between locations that do not exist in reality (a person does not migrate from A to B following a direct path between the two locations).

I. Task E2: Representing flows as networks

Flows between a set of given locations can also be represented as a flow network: locations become vertices, every two locations with movement receive an edge and the number of individuals or trips between each two vertices becomes the weight on the corresponding edge.

Flow networks for marine animals are constructed from passive acoustic telemetry data: vertices of the network are locations of the hydrophones and edges in the network represent movements of tagged aquatic animals (Lédée et al. 2015). Networks are also generated from terrestrial animal Eulerian data, such as camera trap observations (this is limited to species where individuals can be identified from photos and therefore can be tracked between cameras) and high-resolution GPS tracking data (Jacoby and Freeman 2016).

On the human side, flow networks are investigated in networks research in physics as well as in transportation and geography. Physics typically creates these networks from mobile phone data, where any phone moving between two mobile masts is considered as a flow (Expert et al. 2011, Song et al. 2010a). In transportation, flow networks are used to model air or maritime traffic (Hu and Zhu 2009). In geography they typically represent movement of people between a set of geographic areas, such as in case of migration or commuting (Tranos et al. 2015, Farmer and Fotheringham 2011).

Topological properties of networks, such as centrality measures, help identify the characteristics of the movement process that led to a realisation of a specific flow network. In animal context, centrality metrics indicate how often acoustic receivers were visited and how well-connected they are with other receivers. Animal studies use basic centralities such as degree, betweenness, closeness and eigenvector centrality (Lédée et al. 2015, Heupel et al. 2018), while other centralities are not as frequently used

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(Oldham et al. 2019). There is scope for expansion, since some of these alternative centralities capture local information (i.e. how well connected is a vertex with respect to its neighbours), while others identify global connectivity (i.e. how important/central is the vertex for the entire network) and could model movement at different spatial scales. In human mobility, centralities are used in transportation to identify the most well-connected places within a network. Examples include shipping networks (Zhang et al. 2018), air transportation networks (Wang, Mo, Wang et al. 2011) and for public transport smart card data (Zhong et al. 2014). Sometimes networks are also generated from individual GPS trajectories and centralities used for identification of human mobility patterns (Wang, Mei and Cuomo 2019). Centralities are further applied in analysis of movement in team sports, to analyse player interaction networks (Gumundsson and Horton 2017).

An alternative way to investigate a flow network is to compare how similar it is in terms of its properties to a random network or a network with a known structure (e.g. a small-world network, Watts and Strogatz 1998). For animal acoustic flow networks this is done to control for the sampling design of the receiver array rather than for analysis for movement (Lédée et al. 2015). In human mobility, this is a popular way to describe the structure of transportation networks (Hu and Zhu 2009).

Another concept that is frequently used to analyse networks is community detection, a method that uses network structure and the strength of the connections to identify densely connected substructures in the network, called communities (Newman 2006, Fortunato and Hric 2016). Note that a “community” in this context is a mathematical term that denotes a dense region in a network, not to be confused with animal or human communities in a biological or social sense.

The most frequent approach to community detection is node-based, which clusters nodes of the network and creates communities that are not allowed to overlap (i.e. each node is a member of exactly one community) (Palla et al. 2005). This can help find differences between ephemeral aggregations and highly structured social groups in movement of marine animals (Mourier et al. 2012). In public health, node-based community detection has been used to relate patterns in human mobility to spread of infectious diseases (Charaudeau et al. 2014).

Human mobility, in particular geography, use the concept of network communities to identify functional regions, which are spatially contiguous areas where there is more interaction within each area than between areas (Brown and Holmes 1971). Community detection has been used to identify data-driven regions for commuting (Farmer and Fotheringham 2011), migration (Tranos et al. 2015) and for transport flows, such as air traffic (Gegov et al. 2013) or bike flows (Yang et al. 2019).

In human mobility, an important phenomenon is polycentricity in movement (Roth et al. 2011), which means that there exist several groups of locations which generate a large number of flows (both incoming and outgoing), but where the trips from one group are not exclusively assigned to that one particular group (Batty 2013). Polycentricity is a property of cities at all scales (Zhong et al. 2014) and therefore when dealing with urban movement flows, the presence of overlap in the regionalisation is crucial, something that has been known in geography for decades (Goddard 1970). A type of community detection that can address this problem partitions the set of edges instead of the set of nodes and finds edge-based communities (Ahn et al. 2010). This allows creation of overlapping functional regions (Demšar et al. 2014).

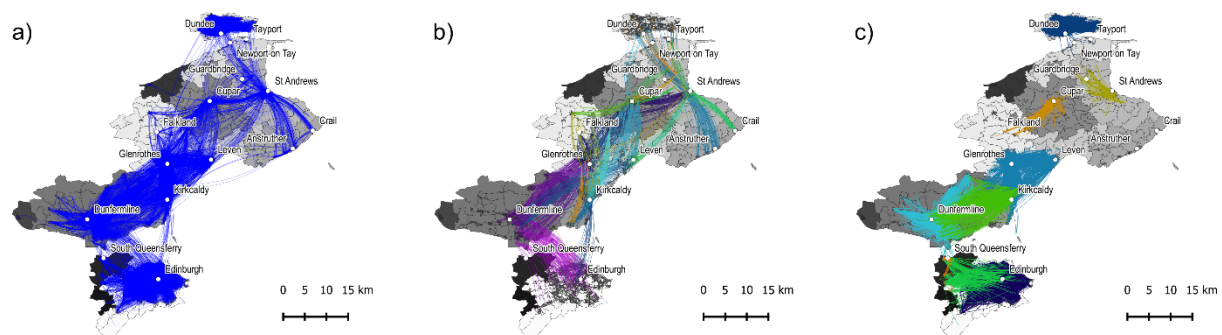


Figure SI1_4. Geographically weighted community detection. Panel a) shows commuting flows between census output areas in the Fife county in Scotland along with output areas in Edinburgh and Dundee (where inhabitants of Fife commute to), which serve as input data into the geographically

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weighted edge-based algorithm. Panel b) shows movement-based communities, that is, those where the majority of flows are between two different locations/places. Panel c) shows place-based communities, that is, those that describe commuting within a given place or town. Grey colours in the background maps indicate non-overlapping communities found with a geographically weighted node-based approach. After Sekulić et al. (2020).

A further development is to consider geography and in particular distance, which is an important factor in human movement decision-making. Community detection methods originate in physics and were initially developed for social networks (Girvan and Newman 2002) and mobile phone networks (Blondel et al. 2015), both of which typically only require information about network structure and do not consider geographic space. Indeed, some physics papers explicitly exclude geography (Expert et al. 2011). However, geographic distance affects individual decision-making and through this the structure of the flow network (Cerina et al. 2012) – in geography this phenomenon is called distance decay (Haggett 1965). To address this, Sekulić et al. (2020) incorporate the length of flows into a community detection algorithm (Figure SI1_4).

Edge-based methods and geographically weighted community detection have to our knowledge not yet been used for animal movement.

J. Task E3: Models and prediction of movement

Movement modelling from Eulerian data is primarily developed for human mobility in geography and transportation, where models using origin-destination flows are known as spatial interaction models. Spatial interaction is a common term for any form of movement or communication over space that results from a decision-making process (Roy and Thill 2005). It can be defined as the movement of people, goods or information and it covers behaviours such as (human) migration, commuting, shopping, recreation, education-related trips, the choice of health care services or patterns of telephone calls. The level of spatial interaction and individual's destination selection is a trade-off between the distance (cost) to a destination and attributes describing characteristics of the origin (propulsiveness) and the destination (attractiveness). An important term in this context is the distance decay effect, which states that strength of interaction between two phenomena decreases with the respective distance (Roy and Thill 2005).

Spatial interaction modelling is unknown in movement ecology. One exception we found is a study that uses spatial interaction models to investigate landscape connectivity (Koenig 2018). There is a potential of using these models with animal Eulerian data, where individuals are identifiable, for example, with camera traps data for uniquely patterned species (see section 4.4. in the main document and section K here).

The first spatial interaction models were called gravity models because of the analogous use of the Newtonian concept of gravity in social physics (Zipf 1946). Stouffer (1940) introduced the concept of intervening opportunities into the gravity model which was able to more accurately represent human migration. As these models attempted to unsuccessfully describe aggregate outcomes from individual level behaviour, Wilson (1971, 1975) introduced the entropy-maximisation family of spatial interaction models. In the next decades, spatial interaction models became popular in physics: to limit the lack of universality in understanding the distance decay in gravity models, Simini et al. (2012) suggested a radiation model which is similar in concept to the intervening opportunities model from geography and considers the opportunities of the traveller rather than the distance travelled (Hong et al. 2019). Recent developments build these models from semantic trajectories: Siła-Nowicka and Fotheringham (2019) introduce a framework for calibrating spatial interaction models using GPS movement data (Figure SI1_5). Spatial interaction also demonstrates an early use of artificial intelligence (neural networks) for movement analysis (Black 1995).

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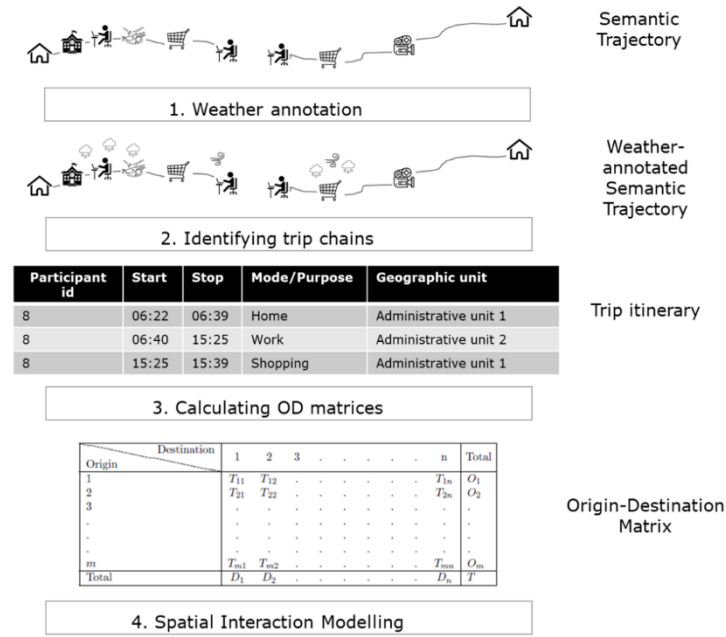


Figure S11_5. A framework for calibrating spatial interaction models from semantically enriched GPS trajectories. 1) GPS trajectories are annotated with weather conditions (precipitation and wind speed). 2) Trip chains are created for each participant from the GPS-based travel survey which involves linking spatially and temporally interrelated trips. 3) Origin-destination matrices can be derived directly from the trip chains where mode, trip purpose and distance between administrative units are known. 4) A number of spatial interaction models can be calibrated (e.g. origin/destination constrained or doubly constrained SIMs). Redrawn after Siła-Nowicka and Fotheringham (2019).

Modelling human population mobility across a range of spatial scales is still a challenge. Recent works (Wang, Kong, Xia et al. 2019, Liu and Yan, 2019) combine individual mobility modelling based on exploratory and preferential returns behaviour with distance-decay and intervening opportunities effects. This creates the so-called unified mobility models (Figure S11_6, Wang, Dong, Cheng et al. 2019) where exploration is weighted by the dynamic population distribution and where individuals are forced to come back to the assigned home location at certain times using their circadian rhythm. The probability of exploring a new location is further weighted by the distance-decay function.

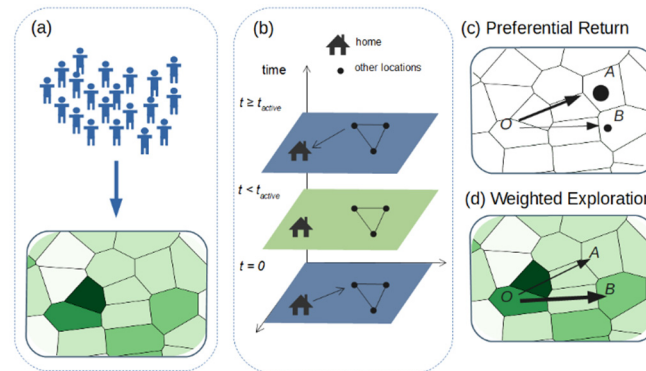


Figure S11_6. The unified mobility model proposed by Wang, Dong, Cheng et al. (2019). a) Individuals are assigned a home location with probability proportional to the population distribution. b) The movement starts and ends at home. When movement occurs, the model selects next the next mobility step to be either c) a preferential return (weighted by the previous visitation frequency) or d) an exploratory step (weighted by the distribution of the population).

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Flow data in marine animal ecology are often analysed using the same types of statistical models as for Lagrangian data (section 3.6. in the main document and section F here). Whoriskey et al. (2019) provides a useful survey with recommendations on which models are suitable for which type of analysis. Examples include state-space models (Dorazio and Price 2018) and various types of Markov models (Papastamatiou et al. 2017), which are sometimes applied using data from a variety of sensors (e.g. accelerometer, magnetometer, depth sensor) along with acoustic array data (Tennesen et al. 2019).

Another common data source for human mobility models are the Call Detail Records data, which log characteristics of communication transactions of mobile phones, in particular which mobile masts they connect to for each transaction. Physicists have used these data to create models and predictions of human mobility flows (Expert et al. 2011, Song et al. 2010a,b). In public health, human movement dynamics from CDR data can also be related to disease incidence and varying spatial and temporal scales and improve understanding of spatial transmissions of disease (Bengtsson et al. 2015, Wesolowski et al. 2016). This has particular applications in the currently on-going pandemic of COVID-19 – Oliver et al. (2020a) discuss the potential of these data to support and control measures of social distancing and how governments and public health authorities can take advantage of technical developments.

K. Task E4: Modelling spatio-temporal dynamics of populations

In ecology, one of the most frequent and longstanding approaches are capture-recapture methods, which have been employed for almost a century (Lincoln, 1930) to estimate demographic parameters, survival and migration. To collect these data, biologists capture, mark and release a sample of the animal population followed by another capture in the following observation season. The proportion of previously marked animals in the newly recaptured group is then used to estimate population size or its dynamic parameters (Otis et al. 1978). Capture-recapture methods directly estimate animal density, space use and landscape connectivity, while they also provide information on general patterns of movement, such as migration pathways and changes in these in response to climate change (Tombre et al. 2019).

In context of movement analysis, capture-recapture is used on data from remote sensing camera traps (Sollmann 2018, Glover-Kapfer et al. 2018). As the basic capture-recapture does not consider the spatial structure of the ecological process (Royle et al. 2013), an adaptation is spatial capture-recapture (SCR), which includes a spatially explicit model for the space use of the individual (Royle et al. 2013, Sollmann, 2018). SCR for camera trap data models spatially explicit encounter probabilities based on the camera traps spatial information, the distances between the camera traps and individual's activity centre (i.e. the midpoint of an individual's home range). SCR and camera traps rely on the individual identification using the natural patterned coat of the animal such as tigers (*Panthera tigris*, Royle et al. 2009), Pampas cats (*Leopardus pajeros*, Gardner et al. 2010) or marten (*Martes*, Sirén et al. 2016) or by using additional tags (e.g. tags earing, GPS collars) (Jacques et al. 2019).

These approaches are less common in human mobility, although there are individual studies that use similar spatially-explicit models for RFID data in sports events (e.g. the 100km march Dodentocht, Van Nieuland et al. 2016) and a recent MSc thesis that uses mark-recapture methods to estimate human population from mobile phone data (Papacharalampous 2014).

In human mobility, understanding crowd movements from Eulerian data is an important area of research in transportation, urban design and mobility research (Abedi et al. 2015). Collective human behaviour is studied using data from Wi-Fi or Bluetooth arrays (Versichele et al. 2012a, Faragher and Harle, 2014) using proximity detection methods. Bluetooth and Wi-Fi data can be used to understand movement patterns of individuals in buildings (Ruiz-Ruiz et al. 2014, Prentow et al. 2015); to detect leaders in groups (Kjærgaard et al. 2013); to study road traffic monitoring and management (Friesen and McLeod, 2015); and to estimate crowd dynamics at large events (Versichele et al. 2012a,b, 2013) or during evacuations and other situations where panic is involved (Kholshchevnikov and Samoshin 2008).

Another type of Eulerian data that are used to model human crowd dynamics is video footage from CCTV cameras (Nayan et al. 2019), which are increasingly common in public spaces such as airports,

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parks or shopping centres. In movement context, CCTV camera data is used to count people and to identify normal and anomalous behaviour of crowds (Santhiya et al. 2015).

L. Task E5: Visualising flows

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Flow data visualisations have a long tradition in geography: OD flow maps were first produced in the 19th century (see for example (human) migration maps by Charles John Minard (Friendly 2008)) and became popular in quantitative geography decades ago (Tobler 1987). More recent developments include space-filling OD maps (Wood et al. 2010), bicycle flow visualisations (Beecham and Wood 2015), flow maps with edge-bundling (Verbeek et al. 2011) and kriskograms for migration flows (Xiao and Chun 2009). Graser et al. (2018) developed a visual system that works on very large flow data sets and Andrienko et al. (2017a) introduced a visual analytics system where flow visualisations are linked to data mining methods to identify patterns in movement. Batty (2018) gives a review of methods for visualising flows in cities. Graser (2019) provides a tool in QGIS to generate the most commonly used flow maps (with straight flows, curved flows and edge bundling, Figure S11_7).

In ecology, most flow visualisations are related to space use (see section 4.1. in the main document and section H here), for example, Papastamatiou et al. (2018) connect space-time densities with HMM-derived activity probabilities to create activity seascapes (Figure 6 in main text). LaZerte et al. (2017) provide a basic mapping system for data from an array of static sensors. A further example of visualising yet another type of Eulerian data in ecology are vector field visualisations of meteorological radar data to identify bird migration flows (Shamoun-Baranes et al. 2016).

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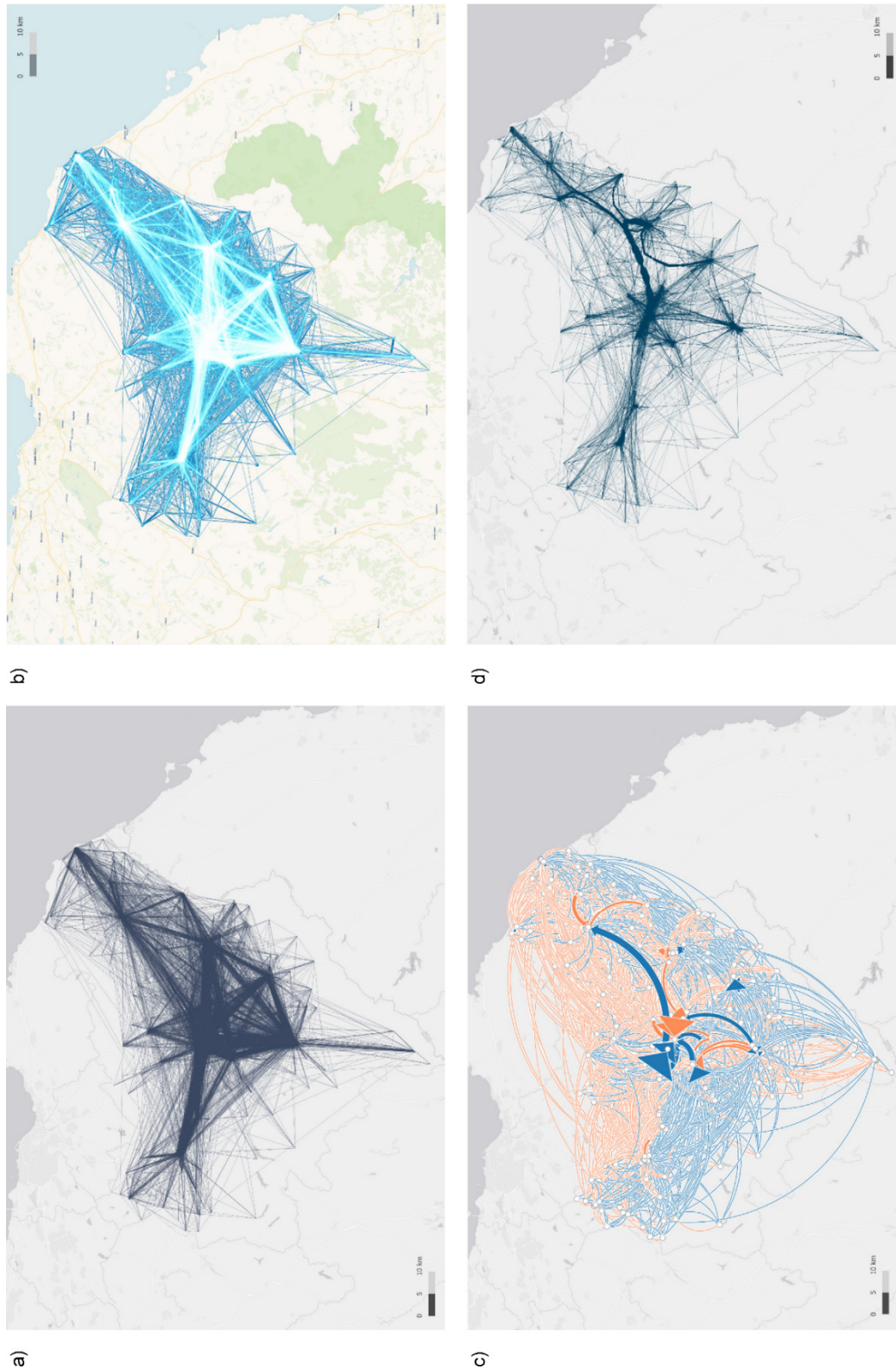


Figure SII_7. Maps of commuting flows in the Borders region in Scotland. Panel a) shows the data in a simple flow map, b) is a flow map where the flow weight (number of commuters) is shown with the intensity and hue of the flow (larger flows are lighter than smaller flows). In c), the size and direction of flows are shown with curved arrows, while d) presents an edge-bundling visualisation, where similar flows are bundled together along a curve. Flow data are available from Scottish Census 2011 (ukdataservice.ac.uk) and maps were created using the open QGIS toolkit by Graser (2019).

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