The ecology of human mobility

Mark G. Meekan^{1*}, Carlos M. Duarte², Juan Fernández-Gracia³, Michele Thums¹, Ana M. M. Sequeira⁴, Rob Harcourt⁵ and Víctor M. Eguíluz⁶.

¹Australian Institute of Marine Science, Indian Ocean Marine Research Centre, University of Western Australia (M470), 35 Stirling Highway, Crawley, WA 6009, Australia

²King Abdullah University of Science and Technology (KAUST), Red Sea Research Center (RSRC), Biological and Environmental Sciences and Engineering (BESE), Thuwal, 23955-6900, Saudi Arabia

³Department of Epidemiology, Harvard T.H. Chan School of Public Health, Boston MA, USA

⁴IOMRC and UWA Oceans Institute, The University of Western Australia, School of Animal Biology and Centre for Marine Futures, M470, 35 Stirling Highway, Crawley, WA 6009, Australia.

⁵Department of Biological Sciences, Macquarie University, Sydney 2109 NSW Australia

⁶Instituto de Física Interdisciplinar y Sistemas Complejos IFISC (CSIC-UIB), E07122 Palma de Mallorca, Spain

***corresponding author: m.thums@aims.gov.au**

Abstract

Mobile phones and other geolocated devices have produced unprecedented volumes of data on human movement. Analysis of pooled individual human trajectories using *big data* approaches have revealed a wealth of emergent features that have ecological parallels in animals across a diverse array of phenomena including commuting, epidemics, the spread of innovations and culture, and collective behaviour. Movement ecology, which explores how animals cope with and optimise variability in resources, has the potential to provide a theoretical framework to aid an understanding of human mobility and its impacts on ecosystems. In turn, *big data* on human movement can be explored in the context of animal movement ecology to provide solutions for urgent conservation problems and management challenges.

Keywords (6 max)

Human movement, *Big Data*, Movement Ecology, Optimisation, Social Networks, Constraint

Introduction

Mobility is a central component of human activity, receiving significant allocation of resources, including time, commodities and energy, with transportation now accounting for 20–25% of global energy use [1]. Development of an understanding of the patterns and drivers of human mobility is, therefore, a key to optimising this critical element of human lifestyles in a world increasingly facing resource limitation and growing human impacts on the biosphere.

Until relatively recently, studies of human mobility have focused at the extreme ends of the spectrum of the scale of movement patterns. At the smallest scales (m-km), the field known as human behavioural ecology [2] has applied models of optimal foraging theory derived from animal ecology to identify the key factors shaping foraging subsistence behaviour in hunter-gatherer communities [2]. At the largest scales (1000s km), the drivers of migrations of humans within and between countries have been analysed in terms of optimisation of “push” and “pull” factors [3, 4]. However, these studies focus on only a very limited part of the spectra of human mobility as it occurs in society today, because the majority of these movements occur in the context of the day-to-day existence of the 50% of the world’s population that lives in cities [5]. Empirical studies of human mobility at these scales were galvanised a decade ago in a seminal paper that based inferences on human movement patterns on the analysis of circulation of banknotes in the United States [6] (Figure 1). This contrasts with studies of animal behaviour where technological developments starting with the ring-banding of birds (7) and culminating with state-of-the-art satellite tracking tags (8) (Figure 1) has allowed accurate and detailed tracking of the individuals of many species and has been a major driver of the theory and study of animal movement ecology [7].

From the outset of the study of animal movement it has been deemed ethically acceptable to attach or implant tracking devices to animals to generate detailed datasets of movement patterns. Until very recently, however, this has not been the case for humans, hence the use of proxies for the tracking of human movement patterns such as banknotes [6] or the distribution of family names [8]. However, the arrival of the geolocated smartphone, effectively a tracking device now voluntarily carried by billions of people, has generated massive volumes of geo-referenced movements, which now constitute *big data*. The data from these devices describe human mobility and behaviour with unprecedented resolution, and for the first time

in human history, individual patterns of human movement [9-11] and interactions [12-14] can be revealed at almost every spatial scale with a remarkable degree of detail, immediacy and precision (**Box 1**). With the advent of smartphones and other new technologies such as wearable fitness trackers, data on mobility at scales relevant to the day-to-day lives of the majority of human populations exceeds by many orders of magnitude the combined total of all that is available for any other species on the planet. At the same time, the sheer scale combined with the difficulties of manipulating and analysing this *big data* has meant that the study of patterns in human movements available from these sources has largely been the province of complex systems analysts. Not surprisingly, results have been interpreted using the paradigms, such as broad distributions and complex networks, of a research community dominated by computer scientists and physicists. For the most part, analyses of these data have taken a “data-mining” approach [15] and little effort has been invested in studies that are hypothesis-led or based in ecological theory. We argue that ecological approaches could inform a deeper understanding of the drivers of human mobility given that such data are much wealthier in motivational content than any available for non-human subjects. Only human mobility couples movement patterns both to social media and electronic interactions that can explicitly link movement to individual motivations and outcomes [14, 16]. Together, this can provide unique insights into the relationships between patterns of human mobility and the impact of humans on the ecosystems they inhabit and in so doing, offer solutions to the pressing conservation and management challenges that now confront society. Here, we review the most salient studies of human mobility and show how these contribute towards a framework for the ecology of human mobility.

Human mobility: insights into populations from individual-based data

The accessibility and volume of geo-referenced data sets of individual human movements has propelled the search for emergent patterns at population scales. Below, we provide examples of analyses that have expanded our understanding of patterns in human movement, their links with social structures within societies and show how these reveal parallels to animal studies.

Statistics of displacement

The analysis of individual human trajectories shows that the net displacement of humans between two consecutive positions at time t and $t + \Delta t$ ($\Delta r = |r(t + \Delta t) - r(t)|$) can be described by a power law distribution, $P(\Delta r) \sim \Delta r^{-\alpha}$, where α is a characteristic scaling exponent. Consequently, individual trajectories cannot be easily characterised by a single displacement, since both short and long movements can occur. Such a power law distribution is characteristic of a Lévy distribution (i.e., Lévy flight, or random walks) with the scaling exponent $\alpha < 2$ (e.g. [6, 10]). The underlying scaling of human movement thus conforms to the same pattern described for many animals, notably marine predators. For these species, including sharks, bony fishes, reptiles and seabirds, Lévy flight is a behaviour that optimizes the rate at which an animal encounters prey in patchy environments [17, 18].

Site fidelity

Similar to many animals, the most frequent human movements occur around a small set of highly-visited locations, typically homes, workplaces, shops etc. [19, 20]. A high degree of site fidelity is thus common to the movement of both many animals (e.g. breeding grounds, foraging areas, resting sites) and humans. The displacement range (measured by the gyration radius) for humans can be described by a power law distribution with exponent $\alpha = 1.65$ truncated by an exponential with a characteristic distance of 350 km [10]. This outcome is a

consequence of very heterogeneous mobility patterns, with the majority of individuals moving within a restricted range, whereas others travel over a region that is orders of magnitude larger (with a gyration radius ranging from 1km to 1,000 km). For animals, site fidelity is thought to be an outcome of predictable resource availability [21] and there are clear parallels for human movements given that the urban environments are also very predictable in the distribution of resources (schools, homes, workplaces etc.).

Collective patterns of movement

Aggregation occurs in both animals (e.g. fish, birds, mammals etc.) and humans [22]. The behaviour imposes constraints on movement patterns and a variety of models derived from physics have been used to understand and quantify the collective patterns that emerge from these behaviors. Analyses of commuting fluxes (recursive traveling between home and work) have been a common subject of studies of collective patterns in human mobility. The distributions of these fluxes are heavy-tailed [23-26], that is, distributions whose tails are not exponentially bounded. Spatial distributions of animal movement show similar patterns of recursive travel, in many cases between foraging, resting and reproductive habitats. These distributions of travel have been modelled using approaches based on Brownian motion such as Brownian bridges that aid definition of home ranges and quantify patterns of space use within the range (e.g. [27])

Relationships between human mobility and social interactions within populations and meta-populations

Daily encounters among individuals are the main driver of the formation of social relationships [28]. Individuals tend to spend more time with people who are friends and family, making a strong link between physical location and social relationships. Consequently, the location of any individual can be predicted from the locations of friends and family and bonds of friendship can be predicted from spatial and temporal co-occurrence of multiple individuals that are visited regularly by any individual. The probability of being “socially connected” (i.e., having friendship bonds with others) decays with distance (d) as d^{-a} [29, 30]. Geolocated data on social interactions, derived from telephone communications or interactions through online social networks have been used to measure the relationship of social bonding and geography [30-32]. Bluetooth [33] and radio frequency identification (RFID) tags have been developed that store proximity data in order to map patterns of social networks (the sociopatterns project; <http://www.sociopatterns.org/>) [34]. This latter approach has been used to map contact patterns in schools [35, 36], a hospital ward [37], and conferences [38]. The concept of movement by humans in physical spatial networks [12] has now been expanded into virtual, digital space through the analysis of proximity networks in online virtual worlds [39] and social media platforms [12, 39]. This use of human movement data to understand social interactions is paralleled by a growing interest in the use of multi-individual tracking strategies to study the structure and dynamics of social networks in populations of wild animals [40, 41].

The ecology of human mobility

The examples above suggest that the ecological principles that explain the movement patterns of marine and terrestrial animals also govern human mobility. A central paradigm of the study of animal ecology is that a detailed understanding of movement offers insights into how

variability in the distribution of resources across landscapes affects the performance of individuals and, in turn, population-level demography [42, 43]. We argue that this concept is equally applicable to the study of humans and can provide new insights into emergent behaviors of human populations and the impacts of their movement patterns on the ecology of ecosystems they inhabit. Furthermore, the analytical approaches developed to link mobility to social networks offer a powerful tool for gaining insights into the social organization of animal species [44] (see **Outstanding Questions**). We illustrate these points with key examples below.

Epidemics

Compartmental reaction-diffusion models [45] have long been used to describe the dynamics of population invasion and range expansion in populations of a broad range of species (e.g. [46]). These models are now also being applied to human populations, notably in the context of the dynamics of epidemics, where individuals (or “agents”) are divided into different classes depending on their infectious state. How agents meet and spread the infection follows patterns dictated by human mobility [47] and are thus central to these models. A metapopulation approach is commonly used in order to cope with the computational challenge of having a vast amount of agents that human populations can provide, particularly on whole country or global scales [48]. These models operate both at large scales and also within constrained environments such as hospitals, schools or conference venues and at these smaller scales, have been used to study the spread of disease and to model appropriate health care responses. Recently, Vanhems et al. [49] showed that in a hospital environment, health care workers were the subpopulation of individuals that were more likely to act as “super-spreaders” of contagion and thus should be targeted for vaccination[50]. On larger, global

scales, the impact of multiscale networks of human mobility has been shown to be crucial in the forecasting of infection routes for global pandemics [23, 50, 51]. Notably, these have shown how the advent of air transportation has facilitated epidemic spread. For example, in the Middle Ages the wavefront of infection of the Black Death spread at around 200 km per year [52], whereas today transport rates of humanity have accelerated, so that such fronts no longer exist [23]. Importantly, knowledge of human patterns of mobility and social networks offer the opportunity to model the spread of contagion to reduce the impact of disease [23]. Such models show that epidemics spread quickly to remote locations (through air transportation connections), whereas at local scales, the spread patterns follow highly-frequented routes typical of commuting flows. Understanding the impacts of human transport systems for epidemics is directly relevant to the diffusion of pathogens and invasive species in ecosystems, as many of these rely on human vehicles, notably airplanes, cars and ships for long distance transport. These allow pathogens and invasive species to expand their distributions across natural barriers to movement, broadening their range and impact [53].

Diffusion of innovations, opinions and cultural traits

The diffusion of innovations can be modelled in a manner similar to that of epidemics. The basic premise of the model is that adopters can be classified as innovators or as imitators and the speed and timing of adoption of an innovation depends on both the degree of their innovativeness and strength of imitation among adopters. Both mobility (through face-to-face contact) and social networks contribute to the social contagion of innovations [54].

The diffusion of cultural traits such as words [55], language [56] and opinions [24] have been shown to be dependent on human mobility both in real and digital space (i.e. face-to-face

contacts mediated through movement and online connections), although the dynamics of social interchange might vary. Recent studies have used data bases provided by geo-located tweets to study the stability of culture and the impact of seasonal tourism on the heterogeneity of cultural patterns within society [56]. For animals, the biological and evolutionary significance of social learning has remained a controversial issue, despite clear evidence of this process in fish, reptiles, birds and mammals [57]. The analysis of movement patterns to inform the study of social learning in humans might prove a useful direction for future investigation of parallels between social learning in animals and the development of culture in humans.

Behaviours during stress

In the case of natural disasters or emergencies in confined environments, understanding the collective behaviour of crowds might help devise better strategies to cope with such events [58, 59]. Studies of human movement during panic situations show that optimal strategies for escape from hazardous situations, such as a smoke-filled room, involve a mixture of individualistic behaviour and collective 'herding' instinct [60]. At larger scales, mobile phone data has been used to track the movements of people after the 2010 earthquake and subsequent cholera outbreak in Haiti [61], Hurricane Sandy in the United States [62] and other disasters [59]. Rapid description of such movement patterns via data from mobile phones and other devices could allow aid and disaster relief to be targeted more effectively for communities. Overall, such analyses provide compelling evidence that human escape reactions conform to the patterns of coordinated collective behavior described for animals. These result in the synchronized behaviours exhibited by schooling fish and flocking birds under attack [63]. The finding that animal escape responses rely on rapid and efficient

transfer of information among individuals, and the diffusion of reactions among neighbors [64], might help develop predictive frameworks for the response of humans to emergencies or stress, a major issue for public safety.

Linking human mobility and animal movement for conservation and management outcomes

The analysis and conceptualization of the *big data* produced by geolinked devices and social networks allows patterns of human and animal movement to be superimposed and synthesized to recognize, understand and solve urgent conservation and management problems. Three key examples of this approach are outlined here.

Fishing

Accurate and reliable data on the behaviour of fishers fundamentally underpins the successful management of a fishery. The analysis of big data provided by smartphones and social networks is poised to revolutionize this process, replacing conventional surveys that are limited both in accuracy and in spatial and temporal extent due to cost [65]. Mobile phone apps produce synoptic, real-time data that not only reveals patterns of fishing pressure and catch and effort data [66], but connectivity in movement patterns of fishers that can also be used to track the risk of the spread of invasive species. At the scale of stocks, information from social networks can be used to optimize fishing practices across entire fisheries to minimize bycatch, enhance sustainability and reduce environmental impacts [67]. Globally, the introduction of automatic ship identification systems makes it possible to observe the behaviour and movement patterns of entire fishing fleets and to map compliance with

management strategies. For the first time, this offers a cost-effective means to address the issue of illegal fishing on the high seas [68].

The illegal trade in wildlife

Trade in wildlife is now acknowledged to be a global crisis. The practice is pushing the most valued species to extinction and depriving many developing countries of billions of dollars of resources. The quantities of animals and plants involved are truly staggering, as are the losses to the front-line park ranger community tasked with protecting these resources; it is estimated that over one thousand rangers have been killed in the line of duty during the last decade (UNEP http://www.unep.org/documents/itw/ITW_fact_sheet.pdf).

Geolocated devices can play a key role in combating this trade and in safeguarding the lives of rangers. In India, the smartphone app “Hejji” allows rangers to monitor the movement and sighting patterns of tigers in protected reserves, and to also place encounters in context, by adding information on water resources, forest fires, and importantly, suspicious human activity. Similarly, “Wildapp” is used by rangers in Africa to collate social and environmental data and track movements of rangers and encounter rates with dead animals. Wildapp is producing data vital to determining poaching rates (<https://ilabaficastrathmore.wordpress.com/2016/09/20/the-wild-app-helping-protect-our-wild-animals/>). In Kenya “tenBoma” collates information from rangers, satellite remote sensing and uses mobile phones confiscated from poachers to expose the social networks that facilitate the trade (<http://www.ifaw.org/sites/default/files/IFAW-tenBoma.pdf>). The latter program illustrates an important point; the same *big data* and software platforms that can aid conservation can also facilitate the illegal trade in wildlife.

Human mobility as a threat to animals

Our transport systems are responsible for the deaths of many millions of animals and trillions of insects each year [69]. Road and train networks fragment habitats, form barriers to migration, act as conduits for the spread of invasive species and are a source of light, noise and particulate pollution that alter animal behaviour and survivorship. Dead and injured animals and insects on roads and verges can attract scavengers that are then also at greater risk of mortality [70].

Until recently, mitigation of these effects has been difficult because the quantification of roadkill is time consuming and effort intensive, limiting the spatial and temporal scope of data collection. However, there is a recent proliferation of smartphone apps that apply citizen science approaches to register roadkills. These apps provide data that allows ranking of species vulnerability, seasonal patterns and monitoring and detection of rare species in roadkill. Importantly, the data provided by the apps allows identification of roadkill hot spots and landscape connectivity issues across broad areas, so that managers can take evidence-based actions to mitigate effects. The data can also be used to increase vehicle safety by incorporating warnings of collision hotspots into GPS navigation systems for cars [71]. These issues and mitigation approaches are paralleled in marine systems where ship-strike poses a major threat to marine megafauna (Box 2)

Future insights on human mobility – lessons from animal ecology and solutions for management and conservation

The above examples show how studies of emergent patterns in human trajectories at different spatial scales are consistent with theory and observations derived for animal movement. Thus, ecological movement theory can inform our understanding of biological and social

processes in human societies beyond the phenomenological approach prevalent to date. How do we facilitate this shift? One obvious route forward utilises the approaches of earlier studies that examined the movement patterns of hunter-gatherer societies and large-scale migration patterns [2]. Many of these applied an optimisation framework equivalent to optimal foraging theory in animal ecology [72, 73] to describe and understand the drivers of movement patterns. Such frameworks are clearly applicable to analyses of *big data* because they are robust in the face of differences in patterns of mobility between humans and animals (**Box 3**) and can be applied in contexts well beyond foraging. In some limited circumstances these ideas are already well developed, such as cost and benefit studies of commuting and urban sprawl [74, 75]. However, the new generation of wearable devices and the linking of digital social networks to mobility patterns offers a means to bring a far greater degree of complexity and detail to optimisation studies.

In turn, the flexibility, detail and immediacy of data gathered by smartphones and geolocated devices offers new opportunities to improve management and conservation outcomes for some of the most important ecological issues faced by human society. Minimising adverse impacts and ensuring sustainable harvests of resources is central to humanity's future. The analysis of big data provided by geolocated devices offers a multitude of opportunities because it provides a cheap and simple means to gather comprehensive and synoptic data sets that allow visualisation of patterns and interactions within human movement and social networks at spatial scales that have never been available in the past.

Conclusions

The infiltration of mobile phones into human societies is now almost complete, with 6.8 billion subscribers (i.e. 96 % of the world population in 2013) [9]. The rapidly developing study of the patterns of mobility of human populations derived from the *big data* these and other digital devices provide has many clear parallels with studies of animal movement. However, a key difference between the two fields is that the emergent patterns found by the combined analysis of individual animal trajectories form the evidential basis of the theory of animal movement ecology [76], whereas human studies do not yet have an equivalent theoretical framework that operates across all spatial scales. Some argue that such a framework is unnecessary, because “with enough data, the numbers speak for themselves” [77]. In reality, all explorations of *big data* sift through an array of variables and include only subsets of these in analyses, so that preconceptions of researchers must always influence results [78]. Optimisation theory provides a relevant, simple and transparent framework for this process. Because human mobility data can be linked to social networks, economic transactions and the physiological state of an individual, the currency and constraints both motivating and limiting movement patterns can be explored in very fine detail. The volume, scope and immediacy of this *big data* offers robust and novel insights into some of the major problems surrounding the sustainable use of ecological resources and the minimisation of human impacts on terrestrial and aquatic ecosystems that now confront society.

Box 1. Resolving patterns of human mobility

Human mobility has been studied at different levels of resolution. (A) Individual trajectories of 10,000 people across the USA derived from geolocated twitter data from June 2015. When analysed as random walks, this data reveals scaling laws that describe the paths followed by humans, the most basic being the displacement that occurs in a certain time window,

$(\Delta r = r(t + \Delta t) - r(t))$, whose distribution is heavy-tailed consistent with a power-law $P(\Delta r) \sim \Delta r^{-\alpha}$ of exponent $\alpha = 1.59$ [6] or 1.75 [10]. (B) To illustrate this point, we show the analysis of the worldwide trajectories of 3 million twitter user in June 2015, which shows a displacement distribution consistent with a power law of exponent $\alpha = 1.0$. The inset shows the superdiffusive scaling of the average displacement with time ($\langle \Delta r \rangle(T) \sim T^\beta$, with $\beta = 1.27$).

(C) The network formed by fluxes of people commuting between counties in the US (data from US census 2001 [see <http://www.census.gov>], only the top 20% of the dominant fluxes shown). Fluxes are explained by population distributions and distances between locations (encapsulated by the gravity and radiation models of movement). (D) shows the fit of the data in C (boxplots) to the gravity model (red lines) $N_{ij} \sim A N_i^\alpha N_j^\beta / d_{ij}^\gamma$, where N_{ij} is the number of people living in county i and working in county j , N_i (N_j) is the population of county i (j) and d_{ij} is the distance between the centroids of counties i and j ; with parameters, $\alpha = 0.35$, $\beta = 0.54$ and $\gamma = 2.7$. Top left figure shows the data N_{ij}^D divided by $N_i^\alpha N_j^\beta$ as a function of distance and the other plots show the data N_{ij}^D divided by the model fit N_{ij}^M as a function of distance (top right), population of origin N_i (bottom left) and population of destination N_j .

The knowledge of the laws behind human mobility is used to model processes that are mediated by human interaction (red boxes). For example, spatiotemporal features of election results can be reproduced by simple models that take into account human mobility, particularly the vote-share distributions and spatial correlations (see E). (F) The spatial spread of epidemics is modelled using our knowledge of human mobility. In (F) we illustrate this by showing a calculation of the epidemic risk of dengue fever in Pakistan using data on human mobility and habitat suitability for the animal vector (mosquitos) [79].

Box 2 Ship-strikes and marine megafauna

Maritime traffic volumes and vessel speeds have grown rapidly over the last few decades. Shipping is responsible for the transportation of 90% of global trade [80] and in 2014, there were 89,464 registered vessels undertaking commercial passage [81]. (A) shows the average monthly density of all vessels, calculated on a logarithmic scale per 1 km² grid cell for 2014. There has also been an emergence of new trade routes in areas that were once relatively untrafficked, such as the northern sea route through the high Arctic, where there is projected to be average annual increase in shipping of 20% per year over the next 25 years [82]. The global increase in shipping has led to a corresponding increase in the number of ship-strikes on marine megafauna, particularly those species that spend long periods of time near the surface [83] such as whales, sirenids, turtles, whale (*Rhincodon typus*) and basking (*Cetorhinus maximus*) sharks. There are numerous documented cases of both serious injuries and mortalities caused by ship-strikes on this fauna [84]. Ship-strikes are exacerbated by the size and the speed of vessels and the likelihood of collision increases in situations where high volumes of maritime traffic overlap with areas important to marine megafauna such as migratory corridors, feeding or breeding grounds [84, 85]. This threat is of most concern for small populations in near-shore habitats with high levels of maritime traffic. For example, collisions with vessels are a causative factor that have prevented population recovery in the North Atlantic right whale (*Eubalaena glacialis*) despite the cessation of commercial whaling [86]. Similarly vessels are implicated in the decline in abundance of some whale shark populations [87] and of some marine turtles (e.g. *Chelonia mydas*), that display strong site and migratory route fidelities to areas that overlap with high densities of shipping [88].

Mitigation through mobility.

The combination of fine scale information on ship movements through the AIS system [68], and advances in our understanding of animal movement behaviour through extensive telemetry [7] has enabled real opportunity for effective mitigation. Since U.S. NOAA regulations lowered ship speed limits in the vicinity of right whale habitats in 2008, deaths from vessel strikes have declined [89] and devices such as such as Whale Alert: A Tool for Reducing Collisions Between Ships and Endangered Whales [90] are now being developed to initiate real-time mitigation. *Big data* approaches combined with insights from refinements of animal movement models provide the potential for real-time dynamic and cost effective mitigation of this otherwise growing threat.

Box 3. Similarities and differences in human and animal mobility

“Consider the subtleness of the sea; how its most dreaded creatures glide under water, unapparent for the most part, and treacherously hidden beneath the loveliest tints of azure..... Consider all this; and then turn to this green, gentle, and most docile earth; consider them both, the sea and the land; and do you not find a strange analogy to something in yourself?”

— Herman Melville, Moby-Dick; or, The Whale

The mobility patterns of humans are most similar to those of many marine animals because, through the use of technology, we have escaped the constraints of body size that apply to the movements of most terrestrial species that transport themselves on land [91]. Some of the other species that have also escaped the constraints of terrestrial locomotion are those that are

either deliberately or inadvertently included by humans in their travels, such as microbes, domestic animals and invasive species. Clear examples of convergence in the studies of animal movement and human mobility are the identification of scaling laws that characterise movement patterns such as Lévy flight, the characterisation of spatial patterns in residency such as fidelity, recursive movements, home ranges and in the spread of invasive species and epidemics. In the case of human epidemics the convergence is complete, since the microbe both infects and is transported by the human host. However, these comparisons also reveal a fundamental difference in human and animal search behaviour because today, many human “foraging” movements are directed; humans often know where the item is before they embark on a journey to find it. For example, humans are likely to use prior knowledge or to do a search online to find a restaurant, bar or specific good for sale and then go directly to that place where the service or item is available. Analysis of the most extensive data sets of human movements within cities show that this is the case - the majority of movements within a city by people occur between a home and a workplace [10, 20, 92, 93]. Thus, unlike animals, most human movements might not necessarily involve (at least extrinsic) searching behaviour.

Box 4. Biologging and the internet of things

Predicted growth in the number and capacity of electronic devices will not only increase the amount of data they provide on human mobility, but also the velocity at which it is generated and the complexity of information it contains. Wearable devices, such as the “Fitbit” shown in the photo (A) above provide a new data stream that opens a window into movement and body physiology [94]. This development mirrors the field of biologging in animals [7] where tracking tags (B – southern elephant seals, *Mirounga leonina*, note tag on head of seal) store both location and data from a variety of sensors that can record body position in three

dimensions, internal (e.g. heart rate) and environmental (e.g. temperature, depth, altitude etc.) variables. As they have done for animals, wearable devices will allow the development of theories connecting human behaviour, body condition and health to movement and activity [95, 96]. In turn, this will be coupled with innovations that connect objects within human environments to the internet. Tracking devices are now commonplace not just on people, but also on all forms of transport (e.g. cars, ships, planes) and the environments in which they move are being linked by technologies such as smart grids, smart cities and smart homes. By 2020 it is predicted that human society will have 50 billion internet connected devices, with average ownership of 6.58 devices per person [97]. As a result, humans will move within an environment described as the “Internet of Things” [98]. Data on movement patterns, the internal state of the person moving, the environment traversed, and the mode of transport used will be available at all times and in all environments on the planet, including those that were once both data-poor and costly to monitor. This has implications for many aspects of social organisation and behaviour. It will speed the diffusion of innovations, culture and opinions but also will allow much closer regulation of behaviour. For example, the remoteness and expense of monitoring the open ocean has meant that these environments have long been a haven for illegal fishing. Today, vessels are being equipped with AIS (Automatic Identification Systems) that report positions to satellites to ensure compliance with fisheries regulations [68]. This type of monitoring can be done remotely and at a fraction of the cost of most other types of compliance enforcement.

Glossary

Animal movement ecology describes the patterns, mechanisms, drivers and effects of the movement of whole organisms from mammals to microbes. The movement ecology paradigm, a related concept [76], characterizes animal movement as dependent on four

components: internal state (reason to move), motion (ways to move), navigation (timing and direction of movement) and external factors that can affect the movement.

Big data It is widely agreed [99] that *big data* shares the characteristics of the “three Vs”: *Volume* - data sets are very large and increasing in volume; *Velocity* - data arrives in a continuous stream with ever increasing velocity; and *Variety* – data is provided by a wide range of sources (e.g. sensors, social media, transaction records, video etc.) that is both structured and unstructured.

Collective behaviour in animals refers to the coordinated and emergent behaviours that occur when individuals aggregate into groups. Classic examples are the behaviour of fishes in schools or the flight of flocks of birds. Emergent properties involve the transfer of information among group members and group decision-making so that movements are synchronised.

Data mining is a phenomenological approach to data exploration where there are no *a priori* concepts as to what would be a “useful” outcome from the analysis, such as the support or rejection of theoretical predictions. It can be both predictive, in which case models are used to predict system states are developed directly from the data, or descriptive, where analyses uncover patterns within large data sets.

Optimisation in the study of animal movement ecology is the theory that animals, through natural selection, seek to maximise benefits and minimise costs of decision making in a landscape of variable resources. Two critical elements of this process include *currency* (the factor that the animal must maximise), which in movement contexts is typically energy intake

and *constraints*, which are the limitations placed on the currency, for example search or transit time.

Social networks are typically networks of friends, acquaintances and work or business colleagues that are linked by interpersonal relationships. The term can also apply to the online site or service that serves to create and sustain these interpersonal linkages.

Outstanding questions

Movement studies of animals, particularly those involving telemetry and biologging (see **Box 4**) are now generating *big data*. To what extent can the analytical techniques that have been applied to human mobility now inform and improve the exploration and understanding of animal mobility?

Big data analyses of human movement have been driven by complex system analyses. Animal movement studies provide a framework within which to ask hypotheses about human movement, but to what degree do external drivers produced by the complexity of human sociality, skew the potential outcomes?

The analysis of data sets of constraints and motivations for human movement poses ethical issues, even when these use existing public data sets, because the more detail that is added to the profile of the person that is making a movement, the higher the likelihood that he or she could be individually identified from results. This is an important issue for research that uses *big data* and will be particularly relevant in the context of optimisation studies.

Big data can be used to understand and optimise the management of legitimate activities for resource extraction such as fishing, but can also empower and facilitate illicit and unregulated behaviours that now threaten the future of species and even entire habitats. How do we curb such behaviours when connectivity within the same software platforms can be critical to both the legal and illegal use of resources?

Acknowledgements

The research reported in this publication was supported by King Abdullah University of Science and Technology (KAUST) through the baseline fund and the Award No 63150414 from the Office of Sponsored Research (OSR) and the Australian Institute of Marine Science. AMMS was supported by an IOMRC (AIMS, CSIRO and UWA) Collaborative Post-doctoral Fellowship, JFG by NIH grant U54GM088558-06 (Lipsitch). We thank Ivan D. Gromicho for the artwork in Fig. 1.

References

1. Rodrigue, J.-P. and C. Comtois, *Transportation and energy*, in *The geography of transport systems*, J.-P. Rodrigue, Editor. 2013, Routledge: New York.
2. Borgerhoff Mulder, M. and R. Schacht, *Human behavioural ecology*. eLS, 2012.
3. Black, R., et al., *The effect of environmental change on human migration*. Global Environmental Change, 2011. **21**: p. S3-S11.
4. Kline, D.S., *Push and pull factors in international nurse migration*. Journal of Nursing Scholarship, 2003. **35**(2): p. 107-111.
5. United Nations, D.o.E.a.S.A., Population Division, *World Urbanization Prospects: The 2014 Revision*. 2014, New York: United Nations.
6. Brockmann, D., L. Hufnagel, and T. Geisel, *The scaling laws of human travel*. Nature, 2006. **439**(7075): p. 462-465.
7. Hussey, N.E., et al., *Aquatic animal telemetry: a panoramic window into the underwater world*. Science, 2015. **348**(6240): p. 1255642.
8. Piazza, A., et al., *Migration rates of human populations from surname distributions*. Nature, 1986. **329**(6141): p. 714-716.
9. Blondel, V.D., A. Decuyper, and G. Krings, *A survey of results on mobile phone datasets analysis*. EPJ Data Science, 2015. **4**(1): p. 1-55.
10. Gonzalez, M.C., C.A. Hidalgo, and A.-L. Barabasi, *Understanding individual human mobility patterns*. Nature, 2008. **453**(7196): p. 779-782.

- 581 11. Saramäki, J. and E. Moro, *From seconds to months: an overview of multi-scale*
582 *dynamics of mobile telephone calls*. The European Physical Journal B, 2015. **88**(6): p.
583 1-10.
- 584 12. Eagle, N., A.S. Pentland, and D. Lazer, *Inferring friendship network structure by*
585 *using mobile phone data*. Proceedings of the National Academy of Sciences, 2009.
586 **106**(36): p. 15274-15278.
- 587 13. Stopczynski, A., et al., *Measuring large-scale social networks with high resolution*.
588 PloS ONE, 2014. **9**(4): p. e95978.
- 589 14. Wang, D., et al. *Human mobility, social ties, and link prediction*. in *Proceedings of*
590 *the 17th ACM SIGKDD International Conference on Knowledge Discovery and Data*
591 *Mining*. 2011. ACM.
- 592 15. Wu, X., et al., *Data mining with big data*. Knowledge and Data Engineering, IEEE
593 Transactions on, 2014. **26**(1): p. 97-107.
- 594 16. Lazer, D., et al., *Life in the network: the coming age of computational social science*.
595 Science 2009. **323**(5915): p. 721.
- 596 17. Humphries, N.E., et al., *Environmental context explains Lévy and Brownian*
597 *movement patterns of marine predators*. Nature, 2010. **465**(7301): p. 1066-1069.
- 598 18. Sims, D.W., et al., *Scaling laws of marine predator search behaviour*. Nature, 2008.
599 **451**(7182): p. 1098-1102.
- 600 19. Krumme, C., et al., *The predictability of consumer visitation patterns*. Scientific
601 reports, 2013. **3**.
- 602 20. Song, C., et al., *Limits of predictability in human mobility*. Science, 2010. **327**(5968):
603 p. 1018-1021.
- 604 21. Switzer, P.V., *Site fidelity in predictable and unpredictable habitats*. Evolutionary
605 Ecology, 1993. **7**(6): p. 533-555.
- 606 22. Parrish, J.K. and W.M. Hamner, *Animal groups in three dimensions: how species*
607 *aggregate*. 1997: Cambridge University Press.
- 608 23. Balcan, D., et al., *Multiscale mobility networks and the spatial spreading of infectious*
609 *diseases*. Proceedings of the National Academy of Sciences, 2009. **106**(51): p. 21484-
610 21489.
- 611 24. Fernández-Gracia, J., et al., *Is the Voter Model a model for voters?* Physical review
612 letters, 2014. **112**(15): p. 158701.
- 613 25. Masucci, A.P., et al., *Gravity versus radiation models: On the importance of scale*
614 *and heterogeneity in commuting flows*. Physical Review E, 2013. **88**(2): p. 022812.
- 615 26. Simini, F., et al., *A universal model for mobility and migration patterns*. Nature, 2012.
616 **484**(7392): p. 96-100.
- 617 27. Horne, J.S., et al., *Analyzing animal movements using Brownian bridges*. Ecology,
618 2007. **88**(9): p. 2354-2363.
- 619 28. Toole, J.L., et al., *Coupling human mobility and social ties*. Journal of The Royal
620 Society Interface, 2015. **12**(105): p. 20141128.
- 621 29. Grabowicz, P.A., et al., *Entangling mobility and interactions in social media*. PLoS
622 One, 2014. **9**(3): p. e92196.
- 623 30. Lambiotte, R., et al., *Geographical dispersal of mobile communication networks*.
624 Physica A: Statistical Mechanics and its Applications, 2008. **387**(21): p. 5317-5325.
- 625 31. Lengyel, B., et al., *Geographies of an online social network*. PloS one, 2015. **10**(9): p.
626 e0137248.
- 627 32. Onnela, J.-P., et al., *Geographic constraints on social network groups*. PLoS one,
628 2011. **6**(4): p. e16939.
- 629 33. Eagle, N. and A. Pentland, *Reality mining: sensing complex social systems*. Personal
630 and ubiquitous computing, 2006. **10**(4): p. 255-268.

34. Cattuto, C., et al., *Dynamics of person-to-person interactions from distributed RFID sensor networks*. PloS one, 2010. **5**(7): p. e11596.
35. Fournet, J. and A. Barrat, *Contact patterns among high school students*. PloS one, 2014. **9**(9): p. e107878.
36. Stehlé, J., et al., *High-resolution measurements of face-to-face contact patterns in a primary school*. PloS one, 2011. **6**(8): p. e23176.
37. Isella, L., et al., *Close encounters in a pediatric ward: measuring face-to-face proximity and mixing patterns with wearable sensors*. PloS one, 2011. **6**(2): p. e17144.
38. Barrat, A., et al., *Social dynamics in conferences: analyses of data from the Live Social Semantics application*, in *The Semantic Web—ISWC 2010*. 2010, Springer. p. 17-33.
39. Szell, M., R. Lambiotte, and S. Thurner, *Multirelational organization of large-scale social networks in an online world*. Proceedings of the National Academy of Sciences, 2010. **107**(31): p. 13636-13641.
40. Armansin, N., et al., *Integrating social network analysis and fine-scale positioning to characterise the associations of a benthic shark*. Animal Behaviour, 2016. **115**: p. 245e258.
41. Jacoby, D.M.P. and R. Freeman, *Emerging Network-Based Tools in Movement Ecology*. Trends in Ecology & Evolution, 2016. **31**(4): p. 301-314.
42. Gaillard, J.-M., et al., *Habitat–performance relationships: finding the right metric at a given spatial scale*. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 2010. **365**(1550): p. 2255-2265.
43. Morales, J.M., et al., *Building the bridge between animal movement and population dynamics*. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 2010. **365**(1550): p. 2289-2301.
44. Kurvers, R.H.J.M., et al., *The evolutionary and ecological consequences of animal social networks: emerging issues*. Trends in Ecology & Evolution, 2014. **29**(6): p. 326-335.
45. Kermack, W.O. and A.G. McKendrick. *A contribution to the mathematical theory of epidemics*. in *Proceedings of the Royal Society of London A: mathematical, physical and engineering sciences*. 1927. The Royal Society.
46. Andow, D., et al., *Spread of invading organisms*. Landscape Ecology, 1990. **4**(2): p. 177-188.
47. Funk, S., M. Salathé, and V.A. Jansen, *Modelling the influence of human behaviour on the spread of infectious diseases: a review*. Journal of the Royal Society Interface, 2010. **7**(50): p. 1247-1256.
48. Mata, A.S. and S.C. Ferreira, *Pair quenched mean-field theory for the susceptible-infected-susceptible model on complex networks*. EPL (Europhysics Letters), 2013. **103**(4): p. 48003.
49. Vanhems, P., et al., *Estimating potential infection transmission routes in hospital wards using wearable proximity sensors*. PloS one, 2013. **8**(9): p. e73970.
50. Salathe, M., et al., *Digital epidemiology*. PLoS Comput Biol, 2012. **8**(7): p. e1002616.
51. Tizzoni, M., et al., *On the use of human mobility proxies for modeling epidemics*. PLoS Comput Biol, 2014. **10**(7): p. e1003716.
52. Murray, J., *Mathematical Biology: Spatial Models and Biomedical Applications, volume II*. 2003, Springer-Verlag, Berlin Heidelberg, Germany.
53. Hulme, P.E., *Trade, transport and trouble: managing invasive species pathways in an era of globalization*. Journal of Applied Ecology, 2009. **46**(1): p. 10-18.

54. Toole, J.L., M. Cha, and M.C. González, *Modeling the adoption of innovations in the presence of geographic and media influences*. PloS one, 2012. **7**(1): p. e29528.
55. Lizana, L., et al., *Modeling the spatial dynamics of culture spreading in the presence of cultural strongholds*. Physical Review E, 2011. **83**(6): p. 066116.
56. Mocanu, D., et al., *The Twitter of Babel: Mapping world languages through microblogging platforms*. PloS one, 2013. **8**(4): p. e61981.
57. Laland, K.N. and V.M. Janik, *The animal cultures debate*. Trends in Ecology & Evolution, 2006. **21**(10): p. 542-547.
58. Kryvasheyev, Y., et al., *Rapid assessment of disaster damage using social media activity*. Science Advances, 2016. **2**(3): p. e1500779.
59. Wang, Q. and J.E. Taylor, *Patterns and limitations of urban human mobility resilience under the influence of multiple types of natural disaster*. PLoS one, 2016. **11**(1): p. e0147299.
60. Helbing, D., I. Farkas, and T. Vicsek, *Simulating dynamical features of escape panic*. Nature, 2000. **407**(6803): p. 487-490.
61. Bengtsson, L., et al., *Improved response to disasters and outbreaks by tracking population movements with mobile phone network data: a post-earthquake geospatial study in Haiti*. PLoS Med, 2011. **8**(8): p. e1001083.
62. Wang, Q. and J.E. Taylor, *Quantifying human mobility perturbation and resilience in Hurricane Sandy*. PLoS one, 2014. **9**(11): p. e112608.
63. Procaccini, A., et al., *Propagating waves in starling, *Sturnus vulgaris*, flocks under predation*. Animal Behaviour, 2011. **82**(4): p. 759-765.
64. Rosenthal, S.B., et al., *Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion*. Proceedings of the National Academy of Sciences, 2015. **112**(15): p. 4690-4695.
65. Gutowsky, L.F.G., et al., *Smartphones and Digital Tablets: Emerging Tools for Fisheries Professionals*. Fisheries, 2013. **38**(10): p. 455-461.
66. Papenfuss, J.T., et al., *Smartphones Reveal Angler Behavior: A Case Study of a Popular Mobile Fishing Application in Alberta, Canada*. Fisheries, 2015. **40**(7): p. 318-327.
67. Barnes, M., et al., *Social networks and environmental outcomes*. Proceedings of the National Academy of Sciences of the United States of America, 2016. **113**(23): p. 6466-6471.
68. McCauley, D.J., et al., *Ending hide and seek at sea*. Science, 2016. **351**(6278): p. 1148-1150.
69. Muñoz, P.T., F.P. Torres, and A.G. Megías, *Effects of roads on insects: a review*. Biodiversity and Conservation, 2015. **24**(3): p. 659-682.
70. Trombulak, S.C. and C.A. Frissell, *Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities*. *Revisión de los Efectos de Carreteras en Comunidades Terrestres y Acuáticas*. Conservation Biology, 2000. **14**(1): p. 18-30.
71. Vercayie, D. and M. Herremans, *Citizen science and smartphones take roadkill monitoring to the next level*. Nature Conservation, 2015. **11**: p. 29-40.
72. Charnov, E.L., *Optimal foraging, the marginal value theorem*. Theoretical population biology, 1976. **9**(2): p. 129-136.
73. Perry, G. and E.R. Pianka, *Animal foraging: past, present and future*. Trends in Ecology & Evolution, 1997. **12**(9): p. 360-364.
74. Brueckner, J.K., *Urban sprawl: Lessons from urban economics*. Brookings-Wharton papers on urban affairs, 2001. **2001**(1): p. 65-97.

- 729 75. Nechyba, T.J. and R.P. Walsh, *Urban sprawl*. The Journal of Economic Perspectives, 730 2004. **18**(4): p. 177-200.
- 731 76. Nathan, R., et al., *A movement ecology paradigm for unifying organismal movement* 732 *research*. Proceedings of the National Academy of Sciences, 2008. **105**(49): p. 19052- 733 19059.
- 734 77. Anderson, C. *The end of theory: The data deluge makes the scientific method* 735 *obsolete*. 2008 [cited 2016 25/04/2016]; Available from: 736 http://www.edge.org/3rd_culture/anderson08/anderson08_index.html
- 737 78. Boyd, D. and K. Crawford, *Critical questions for big data: Provocations for a* 738 *cultural, technological, and scholarly phenomenon*. Information, communication & 739 society, 2012. **15**(5): p. 662-679.
- 740 79. Wesolowski, A., et al., *Impact of human mobility on the emergence of dengue* 741 *epidemics in Pakistan*. Proceedings of the National Academy of Sciences, 2015. 742 **112**(38): p. 11887-11892.
- 743 80. International Maritime Organization *About IMO*, see <http://www.imo.org/> 2016.
- 744 81. United Nations Conference On Trade And Development *Review of Maritime* 745 *Transport 2015 (UNCTAD/RMT/2015)*. 2015: United Nations, Geneva. p. 1-108.
- 746 82. Miller, A.W. and G.M. Ruiz, *Arctic shipping and marine invaders*. Nature Clim. 747 Change, 2014. **4**(6): p. 413-416.
- 748 83. Laist, D.W., et al., *Collisions between ships and whales*. Marine Mammal Science, 749 2001. **17**(1): p. 35-75.
- 750 84. Vanderlaan, A.S.M. and C.T. Taggart, *Vessel collisions with whales: the probability* 751 *of lethal injury based on vessel speed*. Marine Mammal Science, 2007. **23**(1): p. 144- 752 156.
- 753 85. Conn, P.B. and G.K. Silber, *Vessel speed restrictions reduce risk of collision-related* 754 *mortality for North Atlantic right whales*. Ecosphere, 2013. **4**(4): p. 1-16.
- 755 86. Kraus, S.D., et al., *North Atlantic Right Whales in Crisis*. Science, 2005. **309**(5734): 756 p. 561.
- 757 87. Speed, C.W., et al., *Scarring patterns and relative mortality rates of Indian Ocean* 758 *whale sharks*. Journal of Fish Biology, 2008. **72**(6): p. 1488-1503.
- 759 88. Hazel, J., et al., *Vessel speed increases collision risk for the green* 760 *turtle Chelonia mydas*. Endangered Species Research, 2007. **3**: p. 103-113.
- 761 89. van der Hoop, J.M., et al., *Vessel Strikes to Large Whales Before and After the 2008* 762 *Ship Strike Rule*. Conservation Letters, 2015. **8**(1): p. 24-32.
- 763 90. Wiley, D., et al., *Whale Alert: A Tool for Reducing Collisions Between Ships and* 764 *Endangered Whales*, in AAA 2015 Annual Meeting. 2015: San Jose, CA.
- 765 91. Tamburello, N., I.M. Côté, and N.K. Dulvy, *Energy and the scaling of animal space* 766 *use*. The American Naturalist, 2015. **186**(2): p. 196-211.
- 767 92. Bagrow, J.P. and Y.-R. Lin, *Mesoscopic structure and social aspects of human* 768 *mobility*. PloS one, 2012. **7**(5): p. e37676.
- 769 93. Csáji, B.C., et al., *Exploring the mobility of mobile phone users*. Physica A: Statistical 770 Mechanics and its Applications, 2013. **392**(6): p. 1459-1473.
- 771 94. Gibney, E., *The inside story on wearable electronics*. Nature, 2015. **528**(7580): p. 26- 772 28.
- 773 95. Beiwinkel, T., et al., *Using Smartphones to Monitor Bipolar Disorder Symptoms: A* 774 *Pilot Study*. JMIR mental health, 2016. **3**(1): p. e2.
- 775 96. Onnela, J.-P. and S.L. Rauch, *Harnessing Smartphone-Based Digital Phenotyping to* 776 *Enhance Behavioral and Mental Health*. Neuropsychopharmacology, 2016.
- 777 97. Evans, D., *The internet of things: How the next evolution of the internet is changing* 778 *everything*. CISCO white paper, 2011. **1**: p. 1-11.

- 779 98. Ashton, K., *That 'internet of things' thing*. RFiD Journal, 2009. **22**(7): p. 97-114.
780 99. Ward, J.S. and A. Barker, *Undefined by data: a survey of big data definitions*. arXiv
781 preprint arXiv:1309.5821, 2013.
782

Box 1. Resolving patterns of human mobility

Human mobility has been studied at different levels of resolution. (A) Individual trajectories of 10,000 people across the USA derived from geolocated twitter data from June 2015. When analysed as random walks, this data reveals scaling laws that describe the paths followed by humans, the most basic being the displacement that occurs in a certain time window, ($\Delta r = r(t + \Delta t) - r(t)$), whose distribution is heavy-tailed consistent with a power-law $P(\Delta r) \sim \Delta r^{-\alpha}$ of exponent $\alpha = 1.59$ [6] or 1.75 [10]. (B) To illustrate this point, we show the analysis of the worldwide trajectories of 3 million twitter user in June 2015, which shows a displacement distribution consistent with a power law of exponent $\alpha = 1.0$. The inset shows the superdiffusive scaling of the average displacement with time ($\langle \Delta r \rangle(T) \sim T^\beta$, with $\beta = 1.27$).

(C) The network formed by fluxes of people commuting between counties in the US (data from US census 2001 [see <http://www.census.gov>], only the top 20% of the dominant fluxes shown). Fluxes are explained by population distributions and distances between locations (encapsulated by the gravity and radiation models of movement). (D) shows the fit of the data in C (boxplots) to the gravity model (red lines) $N_{ij} \sim A N_i^\alpha N_j^\beta / d_{ij}^\gamma$, where N_{ij} is the number of people living in county i and working in county j , N_i (N_j) is the population of county i (j) and d_{ij} is the distance between the centroids of counties i and j ; with parameters, $\alpha = 0.35$, $\beta = 0.54$ and $\gamma = 2.7$. Top left figure shows the data N_{ij}^D divided by $N_i^\alpha N_j^\beta$ as a function of distance and the other plots show the data N_{ij}^D divided by the model fit N_{ij}^M as a function of distance (top right), population of origin N_i (bottom left) and population of destination N_j . The knowledge of the laws behind human mobility is used to model processes that are mediated by human interaction (red boxes). For example, spatiotemporal features of election results can be reproduced by simple models that take into account human

mobility, particularly the vote-share distributions and spatial correlations (see E). (F) The spatial spread of epidemics is modelled using our knowledge of human mobility. In (F) we illustrate this by showing a calculation of the epidemic risk of dengue fever in Pakistan using data on human mobility and habitat suitability for the animal vector (mosquitos) [79].

Box 2 Ship-strikes and marine megafauna

A)

Maritime traffic volumes and vessel speeds have grown rapidly over the last few decades.

Shipping is responsible for the transportation of 90% of global trade [80] and in 2014, there were 89,464 registered vessels undertaking commercial passage [81]. (A) shows the average monthly density of all vessels, calculated on a logarithmic scale per 1 km² grid cell for 2014.

There has also been an emergence of new trade routes in areas that were once relatively untrafficked, such as the northern sea route through the high Arctic, where there is projected to be average annual increase in shipping of 20% per year over the next 25 years [82]. The global increase in shipping has led to a corresponding increase in the number of ship-strikes on marine megafauna, particularly those species that spend long periods of time near the surface [83] such as whales, sirenids, turtles, whale (*Rhincodon typus*) and basking (*Cetorhinus maximus*) sharks. There are numerous documented cases of both serious injuries and mortalities caused by ship-strikes on this fauna [84]. Ship-strikes are exacerbated by the size and the speed of vessels and the likelihood of collision increases in situations where high

volumes of maritime traffic overlap with areas important to marine megafauna such as migratory corridors, feeding or breeding grounds [84, 85]. This threat is of most concern for small populations in near-shore habitats with high levels of maritime traffic. For example, collisions with vessels are a causative factor that have prevented population recovery in the North Atlantic right whale (*Eubalaena glacialis*) despite the cessation of commercial whaling [86]. Similarly vessels are implicated in the decline in abundance of some whale shark populations [87] and of some marine turtles (e.g. *Chelonia mydas*), that display strong site and migratory route fidelities to areas that overlap with high densities of shipping [88].

Mitigation through mobility.

The combination of fine scale information on ship movements through the AIS system [68], and advances in our understanding of animal movement behaviour through extensive telemetry [7] has enabled real opportunity for effective mitigation. Since U.S. NOAA regulations lowered ship speed limits in the vicinity of right whale habitats in 2008, deaths from vessel strikes have declined [89] and devices such as such as Whale Alert: A Tool for Reducing Collisions Between Ships and Endangered Whales [90] are now being developed to initiate real-time mitigation. *Big data* approaches combined with insights from refinements of animal movement models provide the potential for real-time dynamic and cost effective mitigation of this otherwise growing threat.

Box 3. Similarities and differences in human and animal mobility

“Consider the subtleness of the sea; how its most dreaded creatures glide under water, unapparent for the most part, and treacherously hidden beneath the loveliest tints of azure..... Consider all this; and then turn to this green, gentle, and most docile earth; consider them both, the sea and the land; and do you not find a strange analogy to something in yourself?”

— Herman Melville, *Moby-Dick; or, The Whale*

The mobility patterns of humans are most similar to those of many marine animals because, through the use of technology, we have escaped the constraints of body size that apply to the movements of most terrestrial species that transport themselves on land [91]. Some of the other species that have also escaped the constraints of terrestrial locomotion are those that are either deliberately or inadvertently included by humans in their travels, such as microbes, domestic animals and invasive species. Clear examples of convergence in the studies of animal movement and human mobility are the identification of scaling laws that characterise movement patterns such as Lévy flight, the characterisation of spatial patterns in residency such as fidelity, recursive movements, home ranges and in the spread of invasive species and epidemics. In the case of human epidemics the convergence is complete, since the microbe both infects and is transported by the human host. However, these comparisons also reveal a fundamental difference in human and animal search behaviour because today, many human “foraging” movements are directed; humans often know where the item is before they embark on a journey to find it. For example, humans are likely to use prior knowledge or to do a search online to find a restaurant,

bar or specific good for sale and then go directly to that place where the service or item is available. Analysis of the most extensive data sets of human movements within cities show that this is the case - the majority of movements within a city by people occur between a home and a workplace [10, 20, 92, 93]. Thus, unlike animals, most human movements might not necessarily involve (at least extrinsic) searching behaviour.

Box 4. Biologging and the internet of things

Predicted growth in the number and capacity of electronic devices will not only increase the amount of data they provide on human mobility, but also the velocity at which it is generated and the complexity of information it contains. Wearable devices, such as the “Fitbit” shown in the photo (A) above provide a new data stream that opens a window into movement and body physiology [94]. This development mirrors the field of biologging in animals [7] where tracking tags (B – southern elephant seals, *Mirounga leonina*, note tag on head of seal) store both location and data from a variety of sensors that can record body position in three dimensions, internal (e.g. heart rate) and environmental (e.g. temperature, depth, altitude etc.) variables. As they have done for animals, wearable devices will allow the development of theories connecting human behaviour, body condition and health to movement and activity [95, 96]. In turn, this will be coupled with innovations that connect objects within human environments to the internet. Tracking devices are now commonplace not just on people, but also on all forms of transport (e.g. cars, ships, planes) and the environments in which they move are being linked by technologies such as smart grids, smart cities and smart homes. By 2020 it is predicted that human society will have 50 billion internet connected devices, with average ownership of 6.58 devices per person [97]. As a result, humans will move within an environment described as

the “Internet of Things” [98]. Data on movement patterns, the internal state of the person moving, the environment traversed, and the mode of transport used will be available at all times and in all environments on the planet, including those that were once both data-poor and costly to monitor. This has implications for many aspects of social organisation and behaviour. It will speed the diffusion of innovations, culture and opinions but also will allow much closer regulation of behaviour. For example, the remoteness and expense of monitoring the open ocean has meant that these environments have long been a haven for illegal fishing. Today, vessels are being equipped with AIS (Automatic Identification Systems) that report positions to satellites to ensure compliance with fisheries regulations [68]. This type of monitoring can be done remotely and at a fraction of the cost of most other types of compliance enforcement.

Outstanding questions

Movement studies of animals, particularly those involving telemetry and biologging (see **Box 4**) are now generating *big data*. To what extent can the analytical techniques that have been applied to human mobility now inform and improve the exploration and understanding of animal mobility?

Big data analyses of human movement have been driven by complex system analyses. Animal movement studies provide a framework within which to ask hypotheses about human movement, but to what degree do external drivers produced by the complexity of human sociality, skew the potential outcomes?

The analysis of data sets of constraints and motivations for human movement poses ethical issues, even when these use existing public data sets, because the more detail that is added to the profile of the person that is making a movement, the higher the likelihood that he or she could be individually identified from results. This is an important issue for research that uses *big data* and will be particularly relevant in the context of optimisation studies.

Big data can be used to understand and optimise the management of legitimate activities for resource extraction such as fishing, but can also empower and facilitate illicit and unregulated behaviours that now threaten the future of species and even entire habitats. How do we curb such behaviours when connectivity within the same software platforms can be critical to both the legal and illegal use of resources?

Figure 1. Timeline of technological advances in animal movement and human mobility. Timeline shows the technological advances from animal movement and human mobility research since 1900 to present. GOOS (Global Ocean Observing System) is a global system for sustained observations of the ocean and includes The Ocean Tracking Network, which is a research effort using a global network of acoustic receivers and implanted acoustic transmitters to study the movement patterns of fish. Pop-up satellite archival tags (PSATs) are data loggers with a means to transmit the collected data via satellite developed for gill breathing animals that spend little time at the surface. The ICARUS Initiative (International Cooperation for Animal Research Using Space) is a new animal tracking antenna on the International Space Station that would allow smaller tags to send data back through the low-orbit satellite. The dollar bill represents the first published paper on human mobility, which tracked records of dollar bills across the US as a proxy for human movement [6].

Figure 1

Highlights

Near universal uptake of smartphones has moved human mobility research into Big Data

This data describes human mobility and behaviour with unprecedented resolution

Applying ecological theory provides a framework to inform and predict human mobility

Applications include but are not limited to epidemics, commuting, crowd behaviour