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Big-data approaches enable increased understanding of animal movement ecology

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One sentence summary

Movement ecology is undergoing a big-data revolution, allowing new insights into the ecology of life on the move.

Abstract

Understating animal movement is essential to elucidate how animals interact, survive and thrive in a changing world. Recent technological advances in data collection and management have transformed our understanding of animal "movement ecology" (the integrated study of organismal movement), creating a big-data discipline that benefits from rapid, cost-effective generation of large amounts of data on movements of animals in the wild. These high-throughput wildlife tracking systems now allow more thorough investigations of variation among individuals and species across space and time, the nature of biological interactions, and behavioral responses to the environment. Movement ecology is rapidly extending scientific frontiers through large inter-disciplinary and collaborative frameworks, providing improved opportunities for conservation and new insights into wild animal movements, their causes and consequences.

Print-page summary

BACKGROUND

Movement is ubiquitous in the natural world. All organisms move, actively or passively, regularly or during specific life stages, due to varied proximate drivers such as meeting energetic demands, social interactions, escaping competition or predation. These movements, altogether, determine individual fitness in dynamic environments. Consequently, movement impacts a myriad of ecological processes and is crucial for preserving biodiversity and for coping with major environmental and climate concerns. Driven by advances in analytical methods and technologies for tracking mammals, birds, fish and other free-ranging animals, mostly vertebrates (hereafter 'wildlife'), movement ecology is now undergoing a rapid transformation into a data-rich discipline, following similar developments in fields such as genomics and earth sciences. This ongoing revolution is being facilitated by cost-effective automated high-throughput animal tracking systems capable of generating massive datasets at high resolution over ecologically-relevant spatiotemporal scales.

ADVANCES

Modern tracking technologies efficiently generate copious, accurate information on multiple individual animals moving in the wild, at scales relevant to the ecological context in which the animal perceives, interacts with, and responds to its physical and biotic environment. Reverse-GPS technologies – primarily using acoustic signals for aquatic animals and radio signals for terrestrial ones – are highly cost-effective high-throughput wildlife tracking systems capable of automatically tracking multiple small animals (e.g., 20 g birds) simultaneously for a relatively long time at high temporal (e.g., 1-s interval) and spatial (e.g., a few meters) resolution, but are usually limited to local to regional (up to 100 km wide) scales. GPS-based technologies are more expensive and limited to larger animals, but are readily available, automatic, long-term, spatially accurate, cover nearly global scales and capable of periods of high temporal resolutions at smaller (local to regional) scales. Other animal tracking technologies, mainly radar and computer vision, are less cost-effective, usually limited to relatively small scales, with individual identification being seldom possible, but they can permit snapshots of accurate, high-resolution movement of multiple individuals of small and large animals. In combination, these high-throughput technologies allow groundbreaking research at the frontiers of behavioral, cognitive, evolutionary and movement ecology, by facilitating previously infeasible exploration of how free-ranging animals move in their natural environments. Key research topics that require big movement

data include: the association of inter-individual variation in movement with behavioral, cognitive and physiological characteristics; the determinants of fine-scale social, competitive or predator-prey interactions within or among species; improving evidence-based management of human-wildlife interactions; and elucidating whether, how and why animals change their behaviors across multiple spatial and temporal scales. With the growing availability and influx of big movement data, mutual cross-disciplinary collaborations among biologists and data scientists can help develop and adjust methodologies for data collection, processing and analysis.

OUTLOOK

Modern high-throughput wildlife tracking technologies are opening a new frontier in biological and ecological research. Their advantages, however, come with costs inherent to all high-throughput systems, particularly computational load, intensive data management and processing, and challenging statistical analyses. These challenges could be met by cross-disciplinary collaborations, enlisting fields with a longer history of big-data, and offering new prospects for development. We advocate a substantial increase in combining observational and experimental approaches in movement ecology, with more studies examining behavioral shifts across spatiotemporal scales and life stages. High-resolution tracking of wild animals is currently restricted to local and regional, rather than global scales, a key limitation that can be addressed by combining low- and high-rate sampling, increased interoperability between manufacturers and technologies, data standardization and sharing, and by large, international research collaborations. Integrating big-data on animals' movements and their environment, collected either by remote sensing systems or by animal-borne sensors themselves, will provide increasingly more detailed insights on animal-environment interactions. Real-time data on the simultaneous movement of multiple individuals of various interacting species could be cost-effectively made available to wildlife managers, to help address crucial issues in biodiversity conservation and ecosystem management.

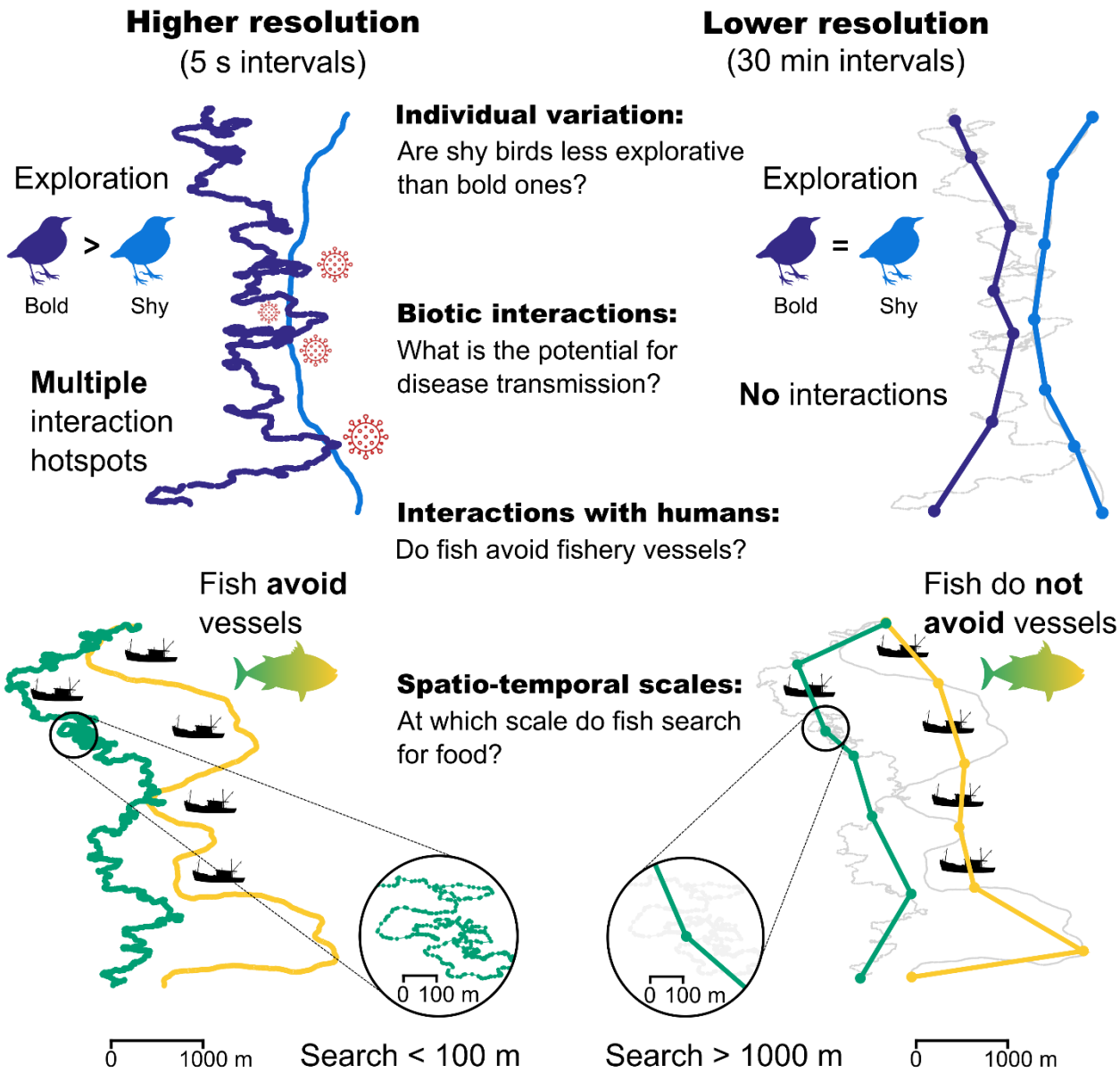

Fig. O: Why do high-throughput movement data matter? Big movement data are essential for addressing key ecological questions, as conclusions based on traditional lower-resolution data could differ markedly from the correct conclusions. We illustrate several examples for contrasting conclusions derived from lower versus higher resolution data of the same tracks from the same number of animals. Only high-resolution data can reveal that bolder birds visit more sites across the landscape, and frequently interact, suggesting high potential for disease transmission, and that fish avoid fisheries, and frequently search locally within small patches. See also Movies S1-5.

Main text

Movement characterizes life. It occurs in all organisms, affects individual fitness, determines evolutionary pathways and shapes ecological processes, including responses to anthropogenic changes. Consequently, studies of animal movement have long been central in ecology, animal behavior and evolutionary and environmental biology. More recently, movement research has experienced a major upsurge with the introduction of a unifying theoretical framework termed "movement ecology" (*1*), and the rapid development of new technologies and data-processing tools (*1-3*). Specifically, recent advances in wildlife tracking techniques have revolutionized our capacity to obtain detailed movement information in space and time across species (*4, 5*) (Fig. 1). With prolific data acquisition, and ongoing advances in the processing of big data, movement ecology is rapidly shifting from a data-poor to a data-rich discipline, similar to previous high-throughput revolutions in diverse fields such as genomics, bioinformatics, nanoscience, biotechnology, cell biology, drug discovery, computer science and environmental monitoring (*6-8*). High-throughput technologies break new ground in addressing long-standing basic-science questions, such as the existence of cognitive maps in wild animals (*9, 10*) and the extreme flight performance of soaring birds (*11, 12*). Furthermore, high-resolution wildlife tracking data uniquely permit direct assessment of how individual animals respond to environmental and anthropogenic changes (*13, 14*).

The engines of the big data revolution in movement ecology: which technologies can finely track animals on the move?

Data on animal movement consist of a time-series of location estimates (*1*), and movement-related covariates (e.g., animal-borne sensor data and auxiliary environmental data). To assess which wildlife tracking techniques can generate big data for movement ecology research, we adjusted four major criteria used to define high-throughput data-collection systems in other scientific fields (*7, 15*). These systems are primarily defined by their ability to collect large amounts of data at a high sampling rate (temporal resolution in the context of movement ecology), as well as long tracking duration, high concurrency (simultaneous tracking of multiple individuals) and high cost effectiveness (total number of localizations per money, effort, or time invested). Thus, based on these four defining criteria, high-throughput technologies in movement ecology are defined as "wildlife tracking systems that provide numerous data on the simultaneous movements of multiple animals, collected at high resolution over relatively long durations in a cost-effective manner". In addition to these four defining criteria, movement ecology studies typically consider other features of wildlife tracking technologies regardless of their ability to generate big data, particularly the

following five key features: spatial scale (range covered by the system), spatial resolution (accuracy and precision), individual/species identification, invasiveness (disruption to tracked animals) and applicability (range of taxa and contexts).

According to the Nyquist–Shannon sampling theorem (*16*), sampling at time interval δt is sufficient to correctly characterize signals (e.g., behaviors, interactions) that typically last $2\delta t$ or longer. In some of our examples, temporal resolution is around 1Hz (δt=1 s), enabling characterization of behaviors and interactions lasting just a few seconds. Unfortunately, the phrase "high-resolution" movement data has been used in the movement ecology literature for a wide range of temporal resolutions, with δt spanning seven orders of magnitude, from tenths of a second to several hours and even days. In this review, we (deliberately) narrowed this range down to encompass a much smaller variation (mostly δt=1-10 s) and report δt for each example. This flexible approach avoids the pitfalls of attempting to find a general standard; rather, research programs in movement ecology should set thresholds for this and the other defining criteria and key characteristics according to the research goals and the key features of the study system (*3*). Beyond the general trend of increased information loss at lower resolution implied by the Nyquist-Shannon criterion, general best-practice guidelines for selecting δt include, for example, substantial underestimation of the total travel distance (and thereby underestimation of the apparent speed) at relatively low resolution typically applied in movement ecology studies (e.g., $\delta t \geq 30$ min), with stronger bias for more tortuous and faster paths (*17, 18*; see also Movie S1). However, the combination of high temporal and low spatial resolution tends to the opposite bias, especially when movement is slow with many stops, due to accumulation of errors (*18, 19*). To alleviate these biases, advanced machine learning methods can be combined with mechanistic agent-based models to capture the relevant resolution and scale of the study system, as we further discuss in the *Data processing and analysis* section.

A rich variety of technologies have been used to gather information on animal movement in the wild (*3, 20*). Over the past two decades, technological advances (Fig. 1A) have yielded much larger datasets than was formerly possible (Figs. 1B and 1C), and tag miniaturization has increased the proportion of species that can be tracked (Fig. 1D). However, wildlife tracking technologies vary in how they tackle the basic trade-offs between the four criteria and other key characteristics. We qualitatively assessed eight common tracking technologies based on our four defining criteria and their main limitations and strengths (Fig. 1A), and quantified their cost-effectiveness as the total number of localizations (the product of the first three criteria) that can be generated based on the same investment (Fig. 1B). These comparisons revealed three fairly distinct groups of high-throughput technologies (see *Data*

collection for details): (a) reverse-GPS systems, including acoustic trilateration of aquatic animals (*21-30*) and radio trilateration of terrestrial animals (*10, 20, 31-35*), regularly meet most criteria, and their main constraint is a relatively limited spatial scale; (b) GPS with upload (*11, 12, 36-42*) and GPS loggers (*9, 43-45*) can meet most criteria under certain circumstances and can track terrestrial (and rarely aquatic) animals at large to global scales, but are usually less cost-effective and less applicable (expensive tags, limited to relatively large animals or to study systems where animals, including small ones, can be recaptured to retrieve data); (c) tracking radars (*46*) and computer vision (*47-51*) can also meet most criteria under certain circumstances and are usually non-invasive, but are less cost-effective, much more restricted in their applicability, spatial range and tracking duration, and specific individuals (and often species) can seldom be identified. Three other technologies – manual triangulation, automated triangulation and geolocators – have relatively low resolutions and do not generate big data, and therefore do not qualify as high-throughput tracking systems.

New big-data frontiers in movement ecology

Ecology, behavior, ontogeny and fitness of individuals

Research under ecologically realistic conditions is imperative for understanding how variation among individual animals shapes ecological, behavioral and evolutionary processes (*52*). Recent research is harnessing high-throughput technologies to quantify behavioral variability in free-ranging individuals, allowing exploration of the causes and consequences of variation among individuals in movement, internal state (e.g., energy status), ontogeny (e.g., maturation and experience), behavioral traits (e.g., personality) or cognitive skills (e.g., spatial memory), as well as trait co-variation patterns and individual fitness (Fig. 2).

Practical difficulties in measuring individual states, traits and behaviors have restricted researchers to conducting studies in controlled, often captive conditions. Yet, reliance on captive animals poses problems of ecological validity (*53*). Wildlife tracking enables greater realism, but behavioral patterns can be missed by traditional low-throughput methods (e.g., Movie S1). Some recent studies have successfully combined extensive yet relatively low-resolution GPS datasets and modeling approaches to infer behavioral variation among individual caribou (*Rangifer tarandus*; δt=1-4 hours) (*54*) and white storks (*Ciconia ciconia*; δt=5 min – 12 hours) (*55*), and an experimental field approach was successfully applied to roe deer (*Capreolus capreolus;* δt=1 hour) (*56*). Despite the relatively low-resolution data, they all met the Nyquist-Shannon criterion such that the applied temporal

resolution successfully captured the mechanisms investigated. High-throughput tracking systems can further transform this line of research by providing detailed fine-scale data from a large number of individuals with known attributes moving simultaneously in their natural landscapes. For example, ATLAS (Advanced Tracking and Localization of Animals in real-life Systems) data (δt=1-8 s) from free-ranging animals revealed evidence for cognitive maps in Egyptian fruit bats (*Rousettus aegyptiacus*) (*9, 10*) and associations between cognitive traits and movement in pheasants (*Phasianus colchicus*) (*32*) (Fig. 2A). Data from high-throughput systems also improves estimates of individual fitness in wild animals, for instance by enabling accurate detection of the location, timing and probable cause of mortality events, even when carcasses are moved by predators (Fig. 2A).

High-throughput technologies also enable new opportunities for investigating how ecological factors may impose physiological challenges on individuals during energy-demanding activities such as foraging, migration, predator-prey interactions or parental care (*25*). For example, acoustic trilateration (δt=9 s) revealed that more active northern pike (*Esox lucius*) were more vulnerable to angling (*30*) (Fig. 2B). Understanding the drivers and consequences of movement and space use may require tracking individuals over long time periods or across different life stages (*57*), hence a somewhat lower temporal resolution. For instance, long-term (11 years) GPS tracking (δt=1-3 min) of northern gannets (*Morus bassanus*) revealed sex-related variation in foraging timing and duration and habitat selection in some years but not in others (*44*).

Biotic interactions

High-throughput systems provide the means to detect social and other intra-specific interactions among individuals in natural environments through simultaneous tracking of most or all group members (*37, 41*), which have previously been difficult to assess (*52*; see also Movie S2). For example, in whole flocks of vulturine guineafowl (*Acryllium vulturinum*) tracked by GPS tags (δt=1 s every fourth day), both dominant and subordinate birds can lead group foraging movements, depending on the resource type being exploited (*41*). Having more detailed data on the movement of the same number of individuals can also illuminate the true nature of inter-specific interactions (Fig, 0), ideally augmented by simultaneous tracking of most or all animals engaged in such interactions (e.g., competitors, predators or prey). This highly challenging need (see *Data collection*) has been acknowledged, for example, in studies of interactions among multiple host, vector and reservoir populations involved in disease transmission (*58*), and also in the context of predator-prey interactions (*59*).

Classic concepts in ecology and animal behavior – such as optimal foraging and ideal free distribution – are based on simplifying assumptions such as context-independent decisions and complete information transfer among individuals, which are often violated in real-life settings (*60*). High-throughput systems enable a more realistic perspective on biotic interactions both within and among species, revisiting existing concepts, and permitting new insights on space-use strategies in competitive or predator-prey relationships (*61*). For example, high-resolution ATLAS data (δt=8 s) revealed robust spatial partitioning among two nearby bat colonies that cannot be explained by commonly hypothesized competition, but could emerge from memory and information transfer (*34*). High-resolution GPS tracking (δt=0.2 s) enabled the assessment of how individual pigeons within coordinated flying groups respond to a robotic predator, providing evidence that refutes the well-established selfish herd hypothesis (*45*). High-resolution data are generally necessary for analyzing interactions with a strong dynamic perspective because encounters (or avoidance) may be cryptic, occasional or ephemeral (*62*). For example, the number of potential predation events (when a predator is in close proximity to its prey) decline exponentially with increasing sampling interval (original δt=1 min), implying that the true nature of predator-prey dynamics among fish cannot be detected by low-throughput data of the same sample size (Fig. 3).

Interactions with natural and anthropogenic environments

Coupled with fine-scale environmental monitoring, high-throughput tracking systems reveal how animals respond to environmental stimuli (Fig. 4, Movies S3-5), providing critical information for developing effective management and restoration actions (*13, 14*). For example, high-resolution GPS (δt=1 s) combined with triaxial accelerometry and atmospheric modeling, were necessary to reveal a differential response of adult and juvenile griffon vultures (*Gyps fulvus*) to challenging soaring conditions (*38*) (Fig. 4A; Movie S3), and whole-lake acoustic trilateration (δt=9 s) revealed interactions with physical features (e.g., water temperature) of a novel environment by non-native wels catfish (*Silurus glanis*) (*27*).

High-throughput tracking data, coupled with mapping of relevant human activities, enable evidence-based conservation and management across diverse ecosystems (*28*). For example, endangered European eels (*Anguilla anguilla*) tracked during downstream migration by acoustic trilateration (δt=1 s) showed a quick behavioral shift upon encountering rapid experimentally induced fluctuations in flow velocity near dams (*23*), which cannot be detected when tracks are sampled at even slightly longer intervals (Fig. 4B; and see another

example in Movie S4). This technology (δt=5 s) also illuminated ecosystem-based effects of recreational activities such as anglers adding feed resources to lakes (*26*). Furthermore, emerging technologies enable rapid, nearly real-time, fine-scale data collection, and have recently been used as early-alert systems, revolutionizing how resources are managed (*63*). For instance, high-resolution GPS tracking of albatrosses (δt=1 min) and condors (δt=30 s) can autonomously and immediately reveal the location of illegal vessels in the ocean (*42*), and of potential collisions with wind turbines (*36; see also Movie S5*), respectively.

Patterns and mechanisms across spatiotemporal scales

Quantifying how movement patterns and drivers change across scales is a major challenge in movement ecology (*1, 64, 65*). In controlled settings, high-throughput methods allowed inference on multiscale behavior of zebrafish (*Danio rerio*) (*66*) and anomalous diffusion in small invertebrates (*48*). Scale-dependent behaviors have also been studied in free-ranging terrestrial and marine animals (*49, 64*), but the relatively low-resolution data used in these studies cannot detect behavior at the fine resolution and scale at which animals typically sense and respond to their environment (*49, 67*).

Black-winged kites (*Elanus caeruleus*) tracked using ATLAS (δt=4 s), for example, showed substantial variation in movement phases at local scales, which remains undetectable even at slightly lower temporal resolution (Fig. 5). This contradicts predictions from the long-debated Lévy flight foraging hypothesis, asserting that animals move in a scale-free manner (*68*). Importantly, high-resolution data enabled distinguishing ergodic from nonergodic processes, a key question in studies of dynamical systems and stochastic processes that has been overlooked in many disciplines (*69*), including movement ecology. In ergodic systems, different segments are equally representative of the whole, hence averaging reveals a typical behavior. Yet, averaging could be misleading in non-ergodic systems, which lack a typical behavior. Assessment of ergodicity is therefore crucial in movement ecology, dictating whether one can infer by ensemble-averaging over multiple movement segments. For foraging raptors, ATLAS revealed a substantial distinction between the ergodic, superdiffusive (faster than diffusive) nature of commuting and the nonergodic, subdiffusive (slower than diffusive) nature of local movement, implying a limited number of ways to commute between distant patches but many ways to hunt or stop within a local patch (Fig. 5) (*35*).

The basic steps in high-throughput movement ecology research

Study design

Movement ecology studies are often based on the field observational approach, documenting the full complexity of natural movement, but with limited capacity to discern and isolate the factors shaping movement variation. The alternative experimental approach is typically applied in controlled laboratory settings, and is less prevalent in studies of animals in the wild. Although field experiments have been conducted with relatively low-resolution movement data (e.g., δt=1 hour; *56*), high-resolution data are necessary for field experiments involving short-term behaviors, fine-scale encounters or multiple interacting individuals/species. High-throughput tracking systems can therefore broaden the scope of experimental movement ecology, creating new opportunities to develop a "laboratories-in-the-wild" experimental approach (*22, 28, 29*).

The two approaches can be combined to address key questions in movement ecology through high-resolution tracking of both manipulated and non-manipulated free-ranging individuals. For example, 149 non-manipulated ATLAS-tracked (δt=1-8 s) Egyptian fruit bats undertook straight shortcuts during their foraging flights, and 23 additional manipulated (transferred to the periphery of their foraging range) bats returned directly to their preferred fruit tree, complementing evidence for a cognitive map (Fig. 6A) (*10*). Similarly, an individual's movement before, during and after an experimental trigger can be compared (*23*) (Fig. 4B). Additionally, individuals with known traits can be introduced to novel wild environments, to test predictions on trait-movement associations. For example, ATLAS-tracked (δt=4 s) juvenile pheasants that exhibited higher spatial cognition under controlled conditions were slower to explore their landscape shortly after release into the wild but showed significant improvement after a few weeks (*32*) (Fig. 2A). Although behavioral and cognitive traits measured in confined controlled versus wild conditions might be similar (e.g., Fig. 6B), trait expression, variability, and among-trait correlations are extremely context-dependent, differing between laboratory and wild conditions (*70*). Finally, individual states can be manipulated and the outcome in the wild monitored to examine long-term consequences of short-term environmental stress. For example, acoustic trilateration (δt=1 min) of largemouth bass (*Micropterus salmoides*) in a lake revealed both a short-term (first few days) response to experimentally induced stress of increased activity, and unexpected long-term (multiple months) carry-over effects rendering stressed fish vulnerable to hypoxia in winter (*21*).

Data collection

Wild animals are tracked using four fundamental methodologies (*20*). Two methodologies use an electronic animal-borne tag that either transmits a signal (transmitter localization),

or receives/senses a signal (receiver/sensor localization). Two other methodologies use animals or tags that reflect either an ambient signal (passive reflection), or one emitted by the tracking system (active reflection) (Fig. 6C). These systems can use radio, acoustic or visual signals, as well as temperature, pressure and other environmental cues. Transmitter localization systems require animal capture and tagging, whereas reflection systems can noninvasively track non-tagged animals. In receiver-sensor localization systems, data are collected on the tag and must be retrieved by remote upload or animal recapture (*9*).

The five high-throughput wildlife tracking technologies (Fig. 1) differ in their compliance with high-throughput criteria. Reverse-GPS systems are transmitter localization systems that track transmitting tags through an array of receivers by time-of-arrival estimation (trilateration). The term "reverse-GPS" emphasizes that like GPS, these are accurate trilateration-based systems, but unlike GPS, raw data and localizations are collected by the system, not on the tag. They use small, energy-efficient and inexpensive tags, which can be used to track multiple animals simultaneously at high spatiotemporal resolution (typically δt=1-10 s, 1-5 m median spatial error) hence regularly provide high-throughput data. These systems include acoustic trilateration of aquatic animals (*21-30*) and radio trilateration of terrestrial animals (e.g., ATLAS; *10, 20, 31-35*). Historically, reverse-GPS techniques were applied to track wildlife >50 years ago (*71, 72*), yet reached high-throughput capacity only following automation during the last decade, and even more recently for terrestrial systems (Fig. 1C). Their main limitations are relatively restricted range (up to 100 km wide) and high installation costs.

GPS and GPS-like systems are receiver localization systems that track tags by trilateration using a satellite constellation. GPS systems with upload retrieve data from tags via a satellite or a cellular link, allowing global coverage at a low-resolution mode (typically δt=15 min to 1 day) and regional coverage (a few hundred km) at high-resolution mode (e.g., *11, 12, 36, 37-40*). Yet, GPS tags are expensive and relatively heavy as satellite/cellular links and onboard localization calculations impose energy costs, limiting these heavier tags to larger animals (though less so with solar charging) and reducing cost-effectiveness. GPS loggers lacking remote upload facilitate collection of high-resolution data (δ=0.1-1 s) from additional sensors (e.g., accelerometers), useful for estimating energy expenditure, identifying behaviors (*73*) and neighbors (*43*), and further refining path resolution through dead reckoning (*74*). Yet, they require animal recapture or tag recollection (*9*), further limiting spatial coverage and applicability.

Tracking radars use active reflection of radio signals, and are capable of collecting extensive movement data of many non-tagged animals simultaneously at high spatiotemporal resolution (e.g., δt=1 s; *46*). However, they rely on expensive and highly specialized radio transceivers, have limited ability to identify species or individuals, and are usually limited to local or regional scales. Computer-vision algorithms based on modern machine learning approaches such as convolutional neural networks, can be applied to track wild birds (e.g., *47*) and fish (e.g., *49, 50, 51*) in their natural habitats at very high spatiotemporal resolution (e.g., δt=0.03 s). However, camera tracking in the wild is typically limited to short ranges, individual's identity is not maintained across videos without natural or artificial marking, tracking multiple individuals is still computationally demanding and time-consuming, and the tracking period is usually short (often up to 30 min) or intermittent.

Data processing and analysis

As in other fields, massive datasets pose a major challenge to manage, process and analyze in a timely manner (*75*). The computing infrastructure needed to store and analyze data is both expensive and generates a large carbon footprint (*33, 76*). Solutions may be inspired from other big-data fields, such as genomics (*6*), remote sensing (*77*) and human mobility (*75*), including robust exploratory data analysis, and automated, reproducible data-processing pipelines (*6*). Big-data exploration can be facilitated by spatial heatmaps of localizations (Fig. 6D), or by plotting individual tracks and distributions of key movement metrics such as speed. These first steps are crucial to identify patterns in the ecological processes observed, and location errors such as outliers (Fig. 6D, 6E).

Pre-processing pipelines can then prepare the full dataset for statistical analyses by filtering unrealistic movement (*33, 76*), after which animal paths can be approximated from raw localizations using smoothing methods (*33*) (Fig. 6E), or by fitting a movement model such as a continuous-time correlated random walk (*28*) (Fig. 6F). Even after removal of technology-induced outliers, accounting for positioning error is critical, and effective error calibration and emerging methods for modeling data error structure can be used to improve positioning estimates of animal movement (*78*). Although position data from high-throughput technologies are generally more accurate than data from low-throughput ones (*17*), the high sampling frequency implies that location errors are autocorrelated, motivating further upgrades of calibration models (*78*), movement metrics (*18*) and space use estimates (*79*). Similar pipelines can be built for movement-associated data such as 3D acceleration (*80*) (Fig. 6G).

Practically, commercial GPS devices nearly always employ on-board data filtering and smoothing algorithms. Similarly, raw data from acoustic trilateration tags are typically processed by proprietary software to obtain position estimates, rendering these procedures a "black-box" for data users. The development and ownership of new high-throughput technologies by movement ecologists themselves, such as Yet-Another-Positioning-Solver (YAPS) (*24*) and ATLAS (*10*), could help the development of transparent and well-documented raw-data processing pipelines. Pipeline reproducibility can be improved by adopting computational science best practices, such as unit testing components for correct data handling, version control, and continuous integration testing (*6, 81*). Increasing pipeline efficiency can allow massive datasets – currently ranging between 10^6 and 10^9 data points per study for basic movement data alone (Fig. 1C) – to be processed on conventional computing hardware. Using compiled languages for pipeline backends and parallel computing can reduce computational times (*6, 77*).

Big data reinforce a trade-off between complex models that aim to adequately mimic individual decision-making in a rich physical or social environment but are challenging to work with, and simpler approaches that are easier to implement but may oversimplify the biological process or suffer from statistical shortcomings such as a lack of uncertainty propagation or inadequate modeling of the autocorrelation structure (*82*). Analytical approaches for movement data include home range analyses (*79*) (Fig. 6G), social network analyses (*37, 41*), and time-varying integrated step-selection functions (*83, 84*) (Fig. 6H). More complex individual-level or group-dynamic movement models such as stochastic differential equations or (hierarchical) hidden Markov models (Fig. 6I) have been developed over the past decade, with user-friendly software packages to aid implementation (*2, 82*). Further methodological advancements allow the identification of how individual foraging attempts are driven by highly dynamic local environments (*85*), and relating individual movement to that of nearby conspecifics (*86*). Individual behaviors can be classified from high-resolution GPS and acceleration data using machine learning algorithms (*39, 40, 73, 87*), and identified behaviors can then be related to individual attributes and/or environmental features (*53, 55, 88*). However, elucidating the drivers of individual movement variation remains challenging (*53*).

One promising approach, recently proposed for related challenges in geographical, social and computer sciences, combines computationally-demanding agent-based models and data-demanding deep learning methods to decode hidden mechanisms from high-throughput data (*89, 90*). Agent-based models can reveal the emergence of system-level patterns from the local-level behaviors and interactions of system components (*91*). Using

genetic algorithms, initial candidate rulesets for individual decision-making can evolve into a robust ruleset that is able to reproduce the unique range and quality of spatial and temporal patterns in high-throughput data ('reinforcement learning', sensu *89*). Such patterns can be revealed by applying machine-learning methods including neural networks and deep learning (*90*). The combination of multiple patterns in high-throughput datasets at different hierarchical levels and scales leads to an unprecedented model robustness, optimized model complexity and reduced uncertainty (*91*). In this pattern-driven process, model specification, calibration and validation steps are all implemented dynamically and iteratively during the model runtime thus enabling a 'learning on the go' (*89*). Overall, the increased availability of high-throughput data will continue to motivate the uptake, refinement and development of novel methods for both data processing and analysis (*3, 84, 86, 87, 92*).

Collaborative networks

By permitting comparisons of animal movement across sites, times, and species, high-throughput technologies can motivate large collaborative networks to address questions on animal adaptations and plastic responses to climate and other environmental changes. Notable examples include the Ocean Tracking Network (*93*), the European Tracking Network (*94*), and the Arctic Animal Movement Archive (*95*). Such collaborative networks and platforms guide the process of establishment and maintenance of tracking infrastructure, facilitate efficient exchange of data, knowledge, analytical tools, software packages and pre-processing pipelines, and offer valuable opportunities in scaling-up study areas, addressing broader ecological questions, training, outreach and funding acquisition (*75, 96*). Enhanced cooperation among traditionally separate disciplines such as ecology, computer science, engineering, bioinformatics, statistical physics, geography and social sciences is crucial for advancing the field, and to facilitate efficient education and outreach.

Major challenges and future directions

Key high-throughput technologies provide the means to characterize, in fine resolution, what individuals do in their natural ecological context. Although low-resolution data might potentially provide equivalent information by increasing sample size (e.g., tracking more individuals), acquiring sufficiently large sample sizes is often impractical and sample size should be kept as low as possible not only for cost considerations but also for ethical reasons. However, despite their very broad scope, high-throughput technologies cannot by themselves cover all aspects of movement ecology research, mostly because they are

practically and naturally limited to studies at regional spatial scales (currently up to 100 km range), and/or intermediate durations (days to a few years). Although advances in tag technologies (miniaturization, energy harvesting, data storage and communication) predict better high-throughput performance (e.g., higher temporal resolution and/or longer periods), spatial scale might remain limited at least in the near future. Projects focusing on larger spatiotemporal scales (e.g., *11, 55, 67*) are inherently confined to low-throughput tracking, with data collected at much lower frequency or at much higher costs per tracked individual, though they may still yield large datasets. These include automatic triangulation systems such as MOTUS (*97*), Doppler-based receiver localization systems (e.g., *98*), the new satellite-based ICARUS system and geolocators (*99*). We thus see high- and low-throughput technologies as complementary rather than competing alternatives, and advocate their integration (*1, 65*). We also call for better integration among high-throughput technologies, and especially between reverse-GPS systems and computer vision, to provide detailed information on both tagged and nontagged interacting animals and their environment. Challenges in integrating contemporary tracking technologies, which hinder progress in addressing both small- and large-scale and single- and cross-taxa questions, as well as attempts to scale up from individual-based information to populations and communities (*100*), could be addressed through better cooperation and coordination between manufacturers and users (*29, 96*). Extending tracking duration and range, ideally to span the lifetime of tracked animals, is important to elucidate how behavior, cognition and physiology develop across spatial and temporal scales and in relation to environmental changes. Accomplishing this goal also requires further technological developments and greater integration of contextual environmental data with high-throughput movement data, linking movement ecology with studies of climate and environmental change.

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List of Supplementary Materials:

Supplementary Text for Figure 1

Full description of procedures and data sources used to construct all parts of Figure 1

Movie S1

Radio trilateration (ATLAS) track of a common noctule bat (*Nyctalus noctula*), illustrating that low-resolution tracking can greatly miss information and bias movement statistics compared to HTME tracking.

Movie S2

Radio trilateration (ATLAS) tracks of a common noctule bat (*Nyctalus noctula*) illustrating that low-resolution tracking can completely miss information on interactions among foraging individuals that is well captured by HTME tracking.

Movie S3

High-resolution GPS tracks of three Griffon vultures (*Gyps fulvus*) climbing thermals, illustrating that HTME can provide highly detailed information on animal behavior, which can be used to assess differential age-dependent responses to fine-scale variation in environmental factors.

Movie S4

Acoustic trilateration (YAPS) track of a downstream-migrating Atlantic salmon (*Salmo salar*) kelt that reached a hydropower facility before spillway gates were opened, and likely depleted its energy reserves due to extensive 22-hr wandering within the reservoir.

Movie S5

High-resolution GPS logger track of a common noctule bat (*Nyctalus noctula*), illustrating that low-resolution tracking can greatly miss information on collision risk of flying animals with wind turbines compared to HTME tracking.

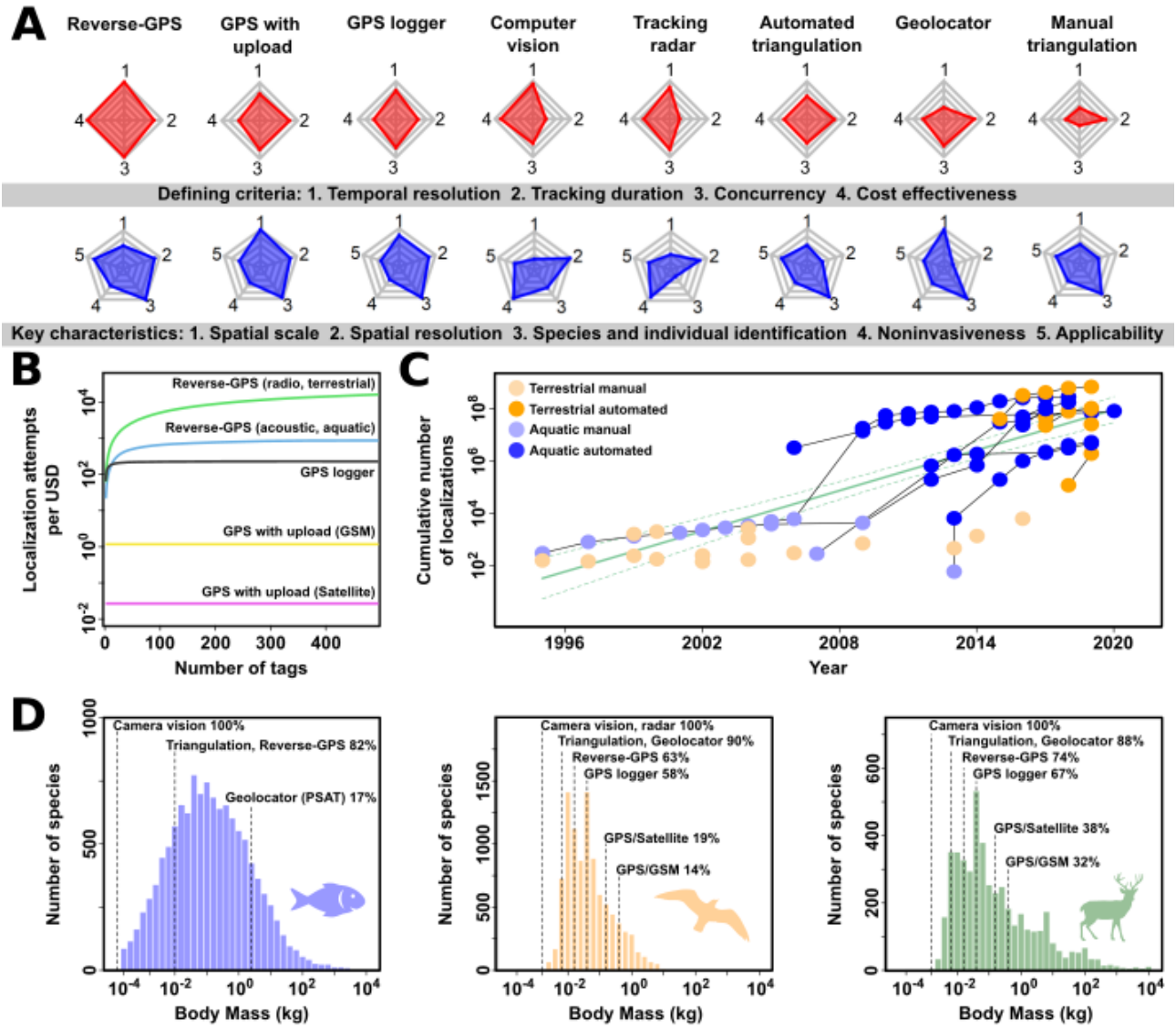

Fig. 1. High-throughput tracking technologies and trends. (A) Qualitative evaluation of the four defining criteria (red) and five key characteristics (blue) of eight major wildlife tracking technologies (ordered by their high-throughput capacity), as estimated by 23 experts. Higher scores represent more favorable high-throughput performance. (B) Cost-effectiveness was quantitatively estimated as the number of localization attempts per investment (USD) for five tag-based tracking systems. (C) Drastic six order-of-magnitude increase in data yields over the past 15 years, marking a shift from manual triangulation to automated reverse-GPS systems in both fish and birds. Each symbol represents a single study/system in a certain year, those linked by black lines represent yields from the same system across years, and the mean trend shown in green with 95% CIs. (D) Proportion of species (tag mass <2% of body mass for fish, <3% for birds and mammals) that can be tracked by the smallest tags currently used to track fish, birds and mammals. For details on estimation procedures and data sources, see Supplementary Material (*101*).

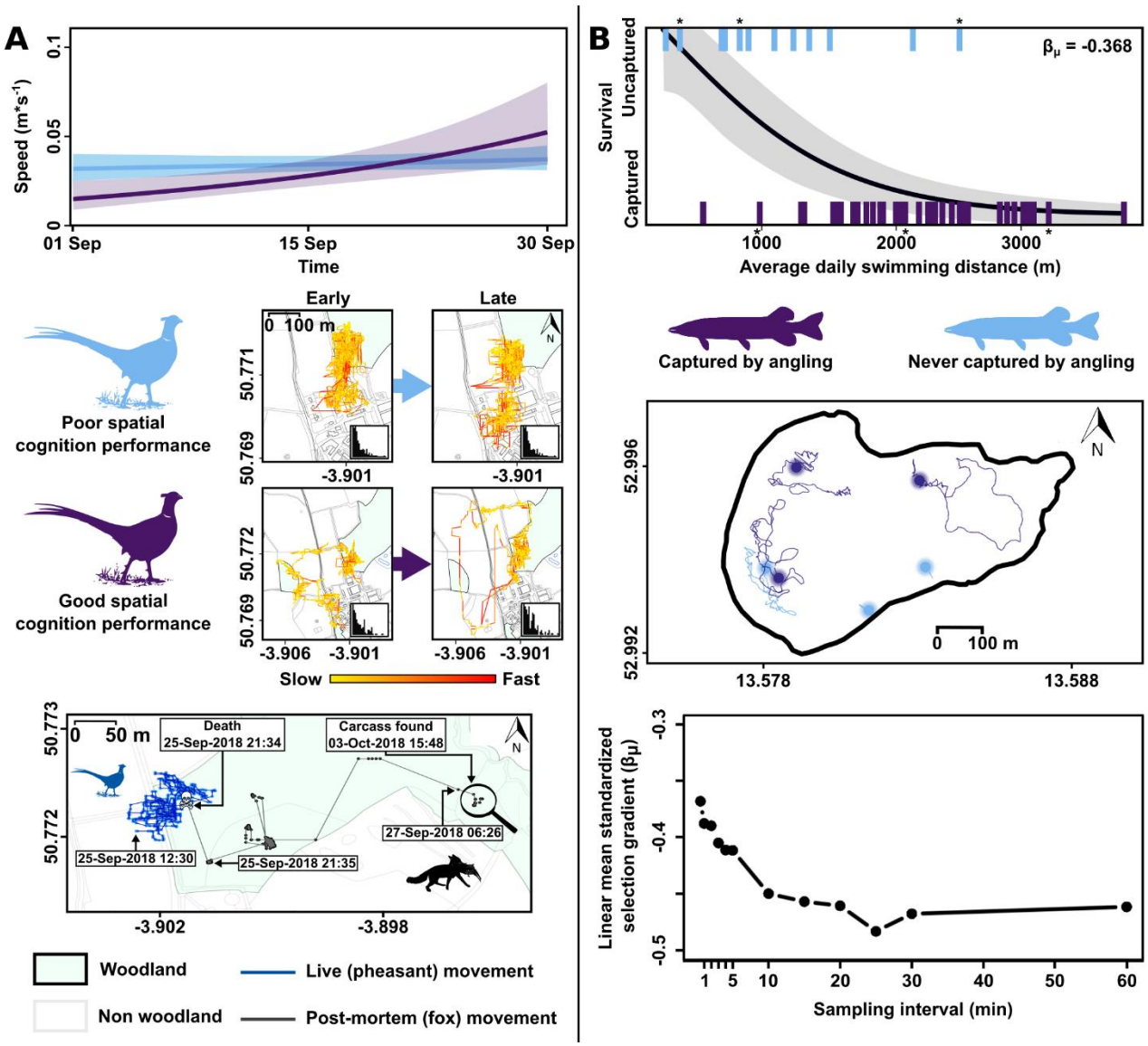

Fig. 2. Inference on patterns of variation in movement, behavior and fitness among individuals, and their potential drivers. (A) ATLAS-tracked (δt=4 s) young pheasants (*Phasianus colchicus*) that performed better in spatial cognitive tasks in captivity made slower transitory movements during the early stages of exploration in the wild but their speed increased with experience of the environment; poor cognitive performers moved faster during early exploration but did not differ in their speed later on (*32*) (top plot). This general trend is illustrated for two representative ATLAS-tracked individuals. Histograms show the number of fast steps (>1 m/s). The bottom map shows a track of a pheasant (blue) that was killed and carried away (with the ATLAS tag) by an untagged fox (*Vulpes vulpes*) (black). ATLAS informed the exact timing and location of such mortality events, whereas *in-situ* observations (skull and crossbones, magnifying glass) would place the mortality location 400 m away with an 8-day uncertainty about its timing in this example. (B) More active northern pike (*Esox lucius*) tracked in the wild using acoustic trilateration (δt=9 s) were more likely to be captured by angling (purple) (top plot), suggesting that angling

pressure results in shyer, less active pike populations (blue) (*30*). Variation in activity between captured and non-captured pike is illustrated in the map by six representative tracks (marked by asterisks in the top plot), with dotted lines representing data gaps (δt>60 s). The strength of harvest selection on fish behavior, represented by the mean-standardized linear selection gradient (β_μ), is rapidly overestimated (more negative values) as temporal resolution decreases (longer sampling intervals) (bottom plot).

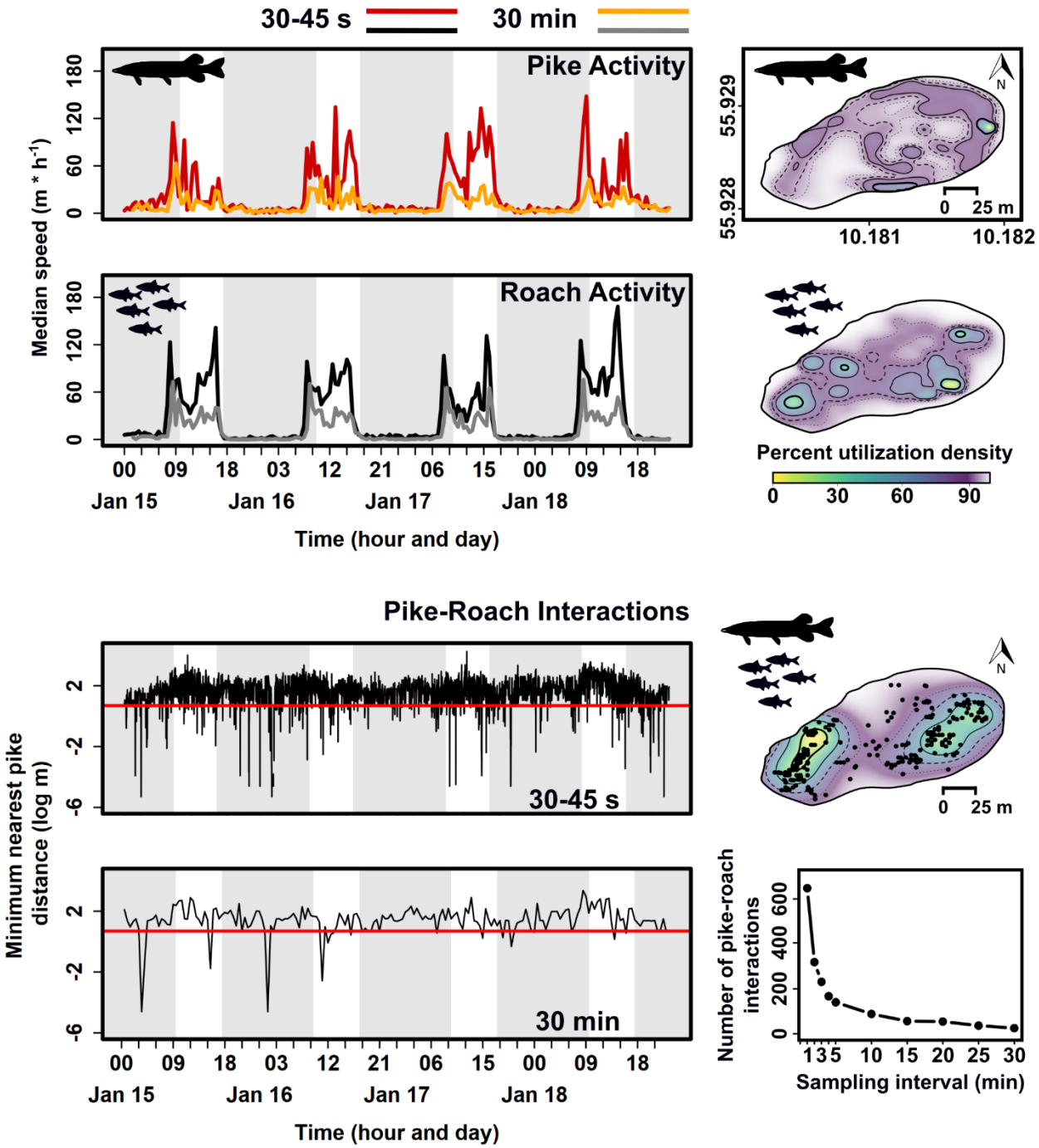

Fig. 3. The nature of biotic interactions. Prey fish (roach, *Rutilus rutilus*, black) were tracked using acoustic trilateration (δt=9 s) simultaneously with predators (northern pike, *Esox lucius*, red). Predators and prey were similar in their diurnal cycles (top plots), but differed in their spatial activity patterns (two top-right maps). Short-range (> 2m) predator-prey encounters occurred throughout all times but more during the night (bottom left plot), and at two large predation hotspots (bottom right map) that only partially overlap with the main activity area of the predators. The number of potential predator-prey encounters is rapidly underestimated as temporal resolution decreases (longer sampling intervals).

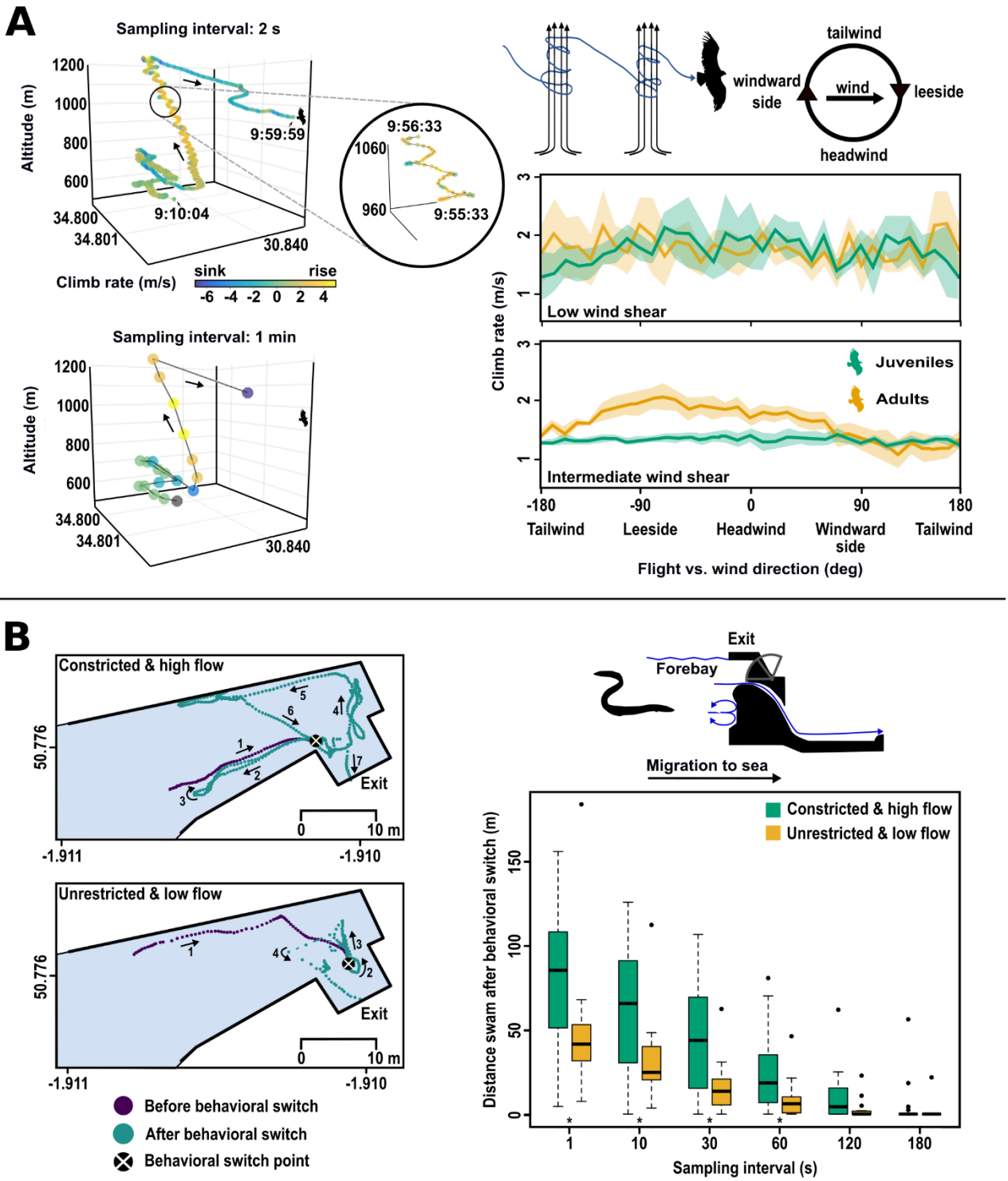

Fig. 4. Insights into the responses of wild animals to their physical environment and to human-induced environmental changes. (A) High-resolution (δt=2 s) GPS tracking of griffon vultures (*Gyps fulvus*) revealed that, under challenging soaring conditions (intermediate wind shear), juveniles climb more slowly in rising-air thermals due to their lower efficiency in circling around wind-drifted thermals compared to adults (*38*). At slightly lower resolution data (δt=1 min), thermal circling disappears. According to the Nyquist-Shannon criterion, a typical circling duration of approximately 15 s (~4 circles min-

[1]; zoomed section) requires $\delta t \leq 7.5$ s. (B) Acoustic trilateration (δt=1 s) revealed that downstream-migrating endangered European eels (*Anguilla anguilla*) shift their behavior from semi-passive downstream swimming to either upstream escape or local search upon encountering experimentally varied flow regime near the exit of a hydropower facility (*23*). A constricted high flow regime generally elicits longer upstream escape (top map), whereas unrestricted low flow leads to shorter spatially confined search for the nearby exit. This difference in behavioral response becomes undetectable and insignificant as sampling interval increases, indicating that relatively high-resolution tracking is required to infer fish response to anthropogenic structures.

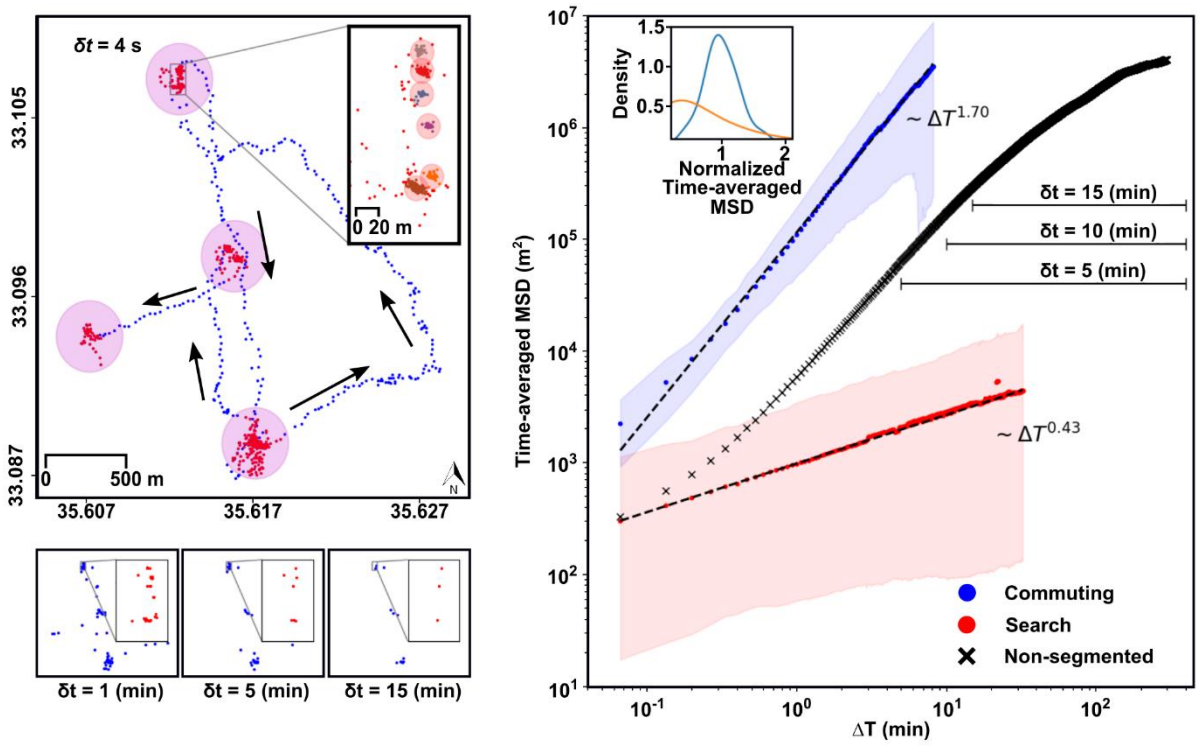

Fig. 5. Detecting commonalities and differences in animal movement and behavior across multiple spatiotemporal scales. Segmentation of a 3.6-hour track of a single black-winged kite (*Elanus caeruleus*) – randomly selected from 155 days of high-resolution (>10^6 localizations) ATLAS tracking (δt=4 s) – reveals (top left map) four segments of area-restricted search (ARS, red dots within purple circles) connected by commuting flights (blue dots, black arrows show direction). Zooming into one ARS (inset) reveals six local clusters (orange circles), which cannot be detected using lower resolution data (bottom left maps) that entail insufficient information (only 34, 7 and 3 ARS localizations for δt=1, 5 and 15 min, respectively), compared to the high-resolution data (δt=4 s; 491 localizations). Time-averaged Mean Square Displacement (MSD) of non-segmented daily tracks recorded across 155 days (black crosses) is not well fitted to a power-law exponent, indicating superdiffusive motion at ΔT<100 min and subdiffusive at ΔT>100 min. Segmenting the track to commuting and ARS (blue and red, shaded areas represent 90% of the trajectories), a clear distinction emerges between superdiffusive ergodic commuting (blue) and subdiffusive non-ergodic ARS (red) (*35*). For the ARS, the distribution of the measured Time-averaged MSD around the mean is large and skewed, indicating nonergodicity (inset, orange line), in contrast to the commuting (inset, blue line). Lower sampling frequencies are insufficient to detect such trends, as they hold information on significantly more limited temporal range, as indicated by the bars for 5, 10 and 15 min.

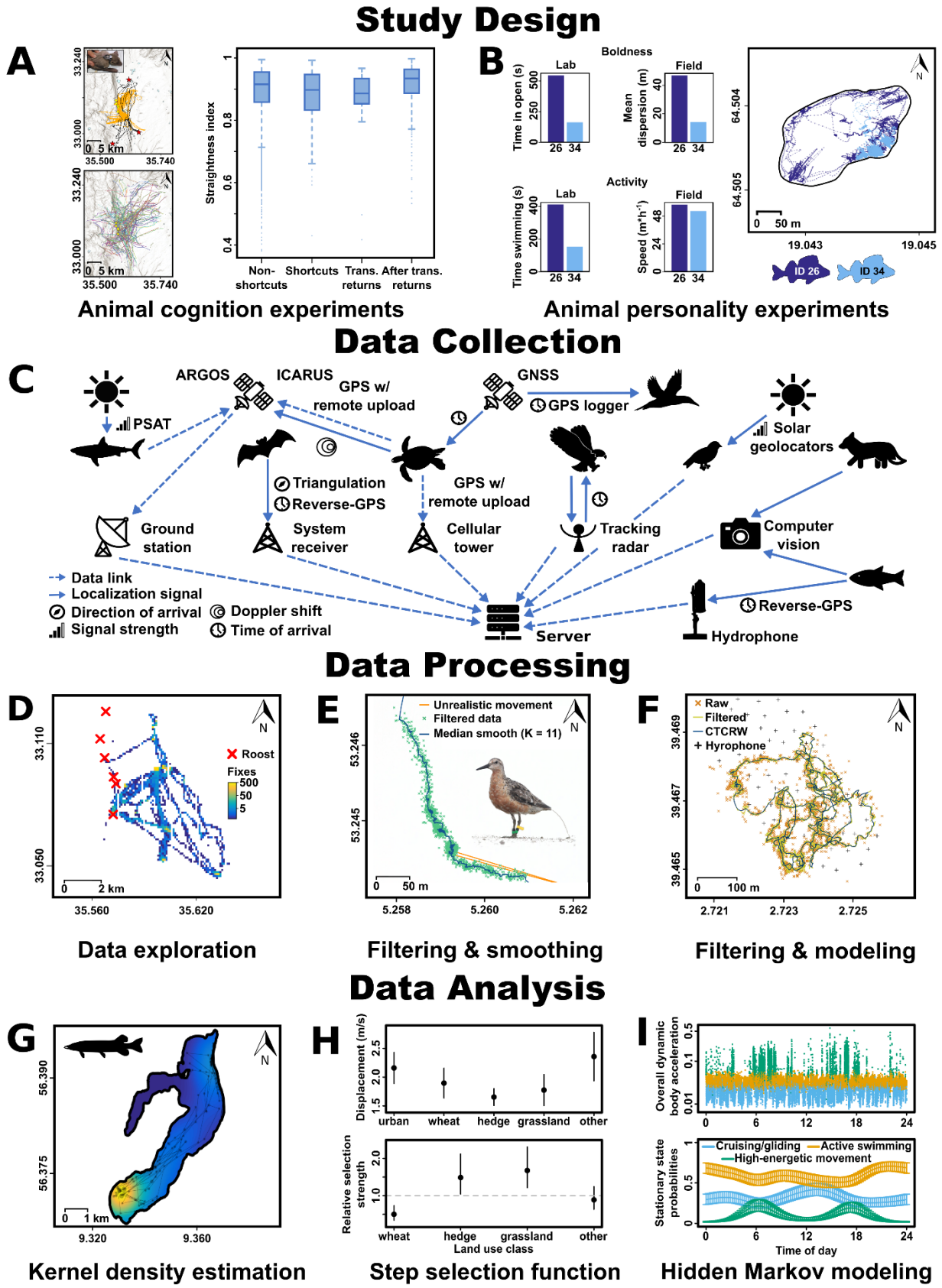

Fig. 6. Key steps in high-throughput movement ecology research. (A) ATLAS - tracked (δt=1-8 s) Egyptian fruit bats (*Rousettus aegyptiacus*) translocated to the periphery of their foraging range returned to their specific foraging tree along straight trajectories (black lines), similar to non-manipulated individuals taking shortcuts, altogether

complementing field evidence for the existence of a cognitive map (*10*). (B) Evidence for consistent difference between bolder and more active (purple) versus shy and less active (blue) European perch (*Perca fluviatilis*), as observed in lab trials, and after release in the wild. (C) An overview of the main wildlife tracking technologies. Referring to the animal icons from left to right and from top to bottom, the illustration shows (shark) popup PSAT tags that report Doppler or solar/temperature geolocation through a satellite data link, (bat) automatic radio triangulation or reverse-GPS tags, (sea turtle) Doppler ARGOS tags and GPS tags that upload location through a satellite or a cellular link or, (eagle) radar tracking, (gannet) GPS logger, (small bird) solar geolocators, (fox) computer vision tracking, (fish) computer vision tracking or ultrasonic aquatic reverse-GPS. Raw datasets are often subject to (D) exploratory data analysis, such as initial assessment of space use by ATLAS-tracked Egyptian fruit bats in relation to roosts and fruit trees, filtered to remove unrealistic movements, and further processed and smoothed as illustrated for (E) ATLAS-tracked (δt=9 s) red knots (*Calidris canutus*) and (F) acoustic trilateration tracking (δt=2-10 s)of a rough ray (*Raja radula*) (*28*). In the following data analysis step, researchers can apply various statistical methods to extract information from high-throughput data to investigate, for example, (G) space use of a pike (*Esox lucius*), using kernel density smoothing and residence patch analysis, (H) habitat selection assessed by applying integrated step-selection function (iSSF) to ATLAS data (δt=8 s) of yellowhammers (*Emberiza citrinella*), revealing that birds move faster in land-use classes that they avoid relative to urban areas, and (I) diel changes in the behavior of an oceanic whitetip shark (*Carcharhinus longimanus*) inferred from acceleration data using a hidden Markov model.