

REVIEW SUMMARY

ECOLOGY

Big-data approaches lead to an increased understanding of the ecology of animal movement

Ran Nathan*, Christopher T. Monk, Robert Arlinghaus, Timo Adam, Josep Alós, Michael Assaf, Henrik Baktoft, Christine E. Beardsworth, Michael G. Bertram, Allert I. Bijleveld, Tomas Brodin, Jill L. Brooks, Andrea Campos-Candela, Steven J. Cooke, Karl Ø. Gjelland, Pratik R. Gupta, Roi Harel, Gustav Hellström, Florian Jeltsch, Shaun S. Killen, Thomas Klefoth, Roland Langrock, Robert J. Lennox, Emmanuel Lourie, Joah R. Madden, Yotam Orchan, Ine S. Pauwels, Milan Říha, Manuel Roeleke, Ulrike E. Schlägel, David Shohami, Johannes Signer, Sivan Toledo, Ohad Vilik, Samuel Westrelin, Mark A. Whiteside, Ivan Jarić

BACKGROUND: Movement is ubiquitous across the natural world. All organisms move, actively or passively, regularly or during specific life stages, as a result of varied proximate drivers including energetic demands, social interactions, competition or predation. Movement closely interacts with individual fitness, affects a myriad of ecological processes, and is crucial for animals' ability to cope with human-induced rapid environmental changes. Driven by advances in analytical methods and technologies for tracking mammals, birds, fish, and other free-ranging vertebrates (hereafter, wildlife), movement ecology is rapidly transforming into a data-rich discipline, following previous developments in fields such as genomics and environmental monitoring. This

ongoing revolution is facilitated by cost-effective automated high-throughput wildlife tracking systems that generate massive high-resolution datasets across scales relevant to the ecological context in which animals perceive, interact with, and respond to their environment.

ADVANCES: Modern tracking technologies efficiently generate copious, accurate information on the movements of multiple individual animals in the wild. Reverse-GPS technologies, which primarily use acoustic signals under water and radio signals over land, are automated high-throughput systems that are highly cost- and power-effective and capable of simultaneous tracking of multiple small animals (e.g., 20-g birds) at high spatiotemporal resolution

(e.g., 1-s interval, a few meters) for months, but they require system installation and are usually limited to regional scales (≤ 100 km wide). GPS-based systems are, by contrast, readily available, longer term, and cover nearly global scales, but are similarly spatially accurate and periodically capable of high-resolution tracking at regional scales. However, they are more cost- and power-demanding, limited to larger animals, and cannot be applied under water. Two other tracking technologies, radar and computer vision, permit high-resolution snapshots of the movement of multiple individuals and can noninvasively track nontagged animals, but are less cost-effective, usually limited to smaller scales, and make individual identification challenging. Combined, these high-throughput technologies enable groundbreaking research in animal behavior, cognitive sciences, evolution, and ecology, facilitating previously infeasible investigation of animal movement ecology. Big movement data can help link interindividual variation in movement to individual behavior, traits, cognition and physiology; divulge fine-scale interactions within or among species; improve evidence-based management of human-wildlife interactions; and elucidate behavioral changes across spatiotemporal scales.

OUTLOOK: High-throughput wildlife tracking technologies are opening new research frontiers in biology and ecology. Their advantages, however, come with typical big-data costs such as computational load, intensive data management and processing, and challenging statistical analyses. Enlisting fields with a longer history of big data offers new prospects to address these challenges. Progress will arise from combining observational and experimental movement ecology and data-rich studies revealing behavioral shifts across individuals, species, scales, ecosystems, and life stages. High-resolution wildlife tracking is currently infeasible at large to global scales, a key limitation that can be addressed by combining low- and high-rate sampling, increasing interoperability between technologies, standardizing and sharing data, and promoting multidisciplinary international collaboration. Coupling movement and environmental big data could help determine impacts of major environmental and climate changes on animal-environment interactions, whereas real-time movement data could uniquely inform biodiversity conservation and ecosystem management. ■

Higher resolution

(5 s intervals)

Exploration



Bold Shy
Multiple interaction hotspots

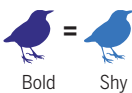
Individual variation:
Are shy birds less explorative than bold ones?

Biotic interactions:
What is the potential for disease transmission?

Lower resolution

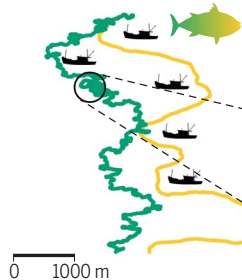
(30 min intervals)

Exploration



Bold Shy
No interactions

Fish **avoid** vessels

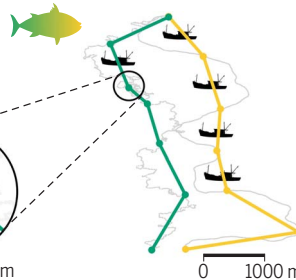


Interactions with humans:
Do fish avoid fishery vessels?

Spatio-temporal scales:
At which scale do fish search for food?

Search < 100 m

Fish do **not avoid** vessels



Search > 100 m

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. Higher-resolution data can reveal that bolder birds visit more sites across the landscape and that bird tracks frequently cross each other, suggesting high potential for disease transmission, and that fish avoid fisheries and frequently search locally within small patches. None of these conclusions, however, could have been drawn from lower-resolution data. See also movies S1 to S5.

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REVIEW

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Big-data approaches lead to an increased understanding of the ecology of animal movement

Ran Nathan^{1,2,*}, Christopher T. Monk^{3,4,5}, Robert Arlinghaus^{5,6}, Timo Adam⁷, Josep Alós⁸, Michael Assaf⁹, Henrik Baktøft¹⁰, Christine E. Beardsworth^{11,12}, Michael G. Bertram¹³, Allert I. Bijleveld¹¹, Tomas Brodin¹³, Jill L. Brooks¹⁴, Andrea Campos-Candela^{5,8}, Steven J. Cooke¹⁴, Karl Ø. Gjelland¹⁵, Pratik R. Gupta^{11,16}, Roi Harel^{1,2}, Gustav Hellström¹³, Florian Jeltsch^{17,18}, Shaun S. Killen¹⁹, Thomas Klefoth²⁰, Roland Langrock²¹, Robert J. Lennox²², Emmanuel Lourie^{1,2}, Joah R. Madden¹², Yotam Orchan^{1,2}, Ine S. Pauwels²³, Milan Říha²⁴, Manuel Roeleke¹⁷, Ulrike E. Schlögel¹⁷, David Shohami^{1,2}, Johannes Signer²⁵, Sivan Toledo^{2,26}, Ohad Vilk^{1,2,9}, Samuel Westrelin²⁷, Mark A. Whiteside^{12,28}, Ivan Jarić^{24,29}

Understanding 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 investigation 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 expanding scientific frontiers through large interdisciplinary and collaborative frameworks, providing improved opportunities for conservation and insights into the movements of wild animals, and their causes and consequences.

Movement characterizes life. It occurs in all organisms, affects individual fitness, determines evolutionary pathways, and shapes ecological processes, including responses to anthropogenic change. 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) in addition to 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 change (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 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 amount of money, effort, or time invested). Thus, on the basis of 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 and 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 and interactions) that typically last $2\delta t$ or longer. In some of our examples, the temporal resolution is ~ 1 Hz ($\delta t = 1$ s), which enables characterization of behaviors and interactions lasting just a few seconds. Unfortunately, the phrase “high-resolution movement data” has been used in movement

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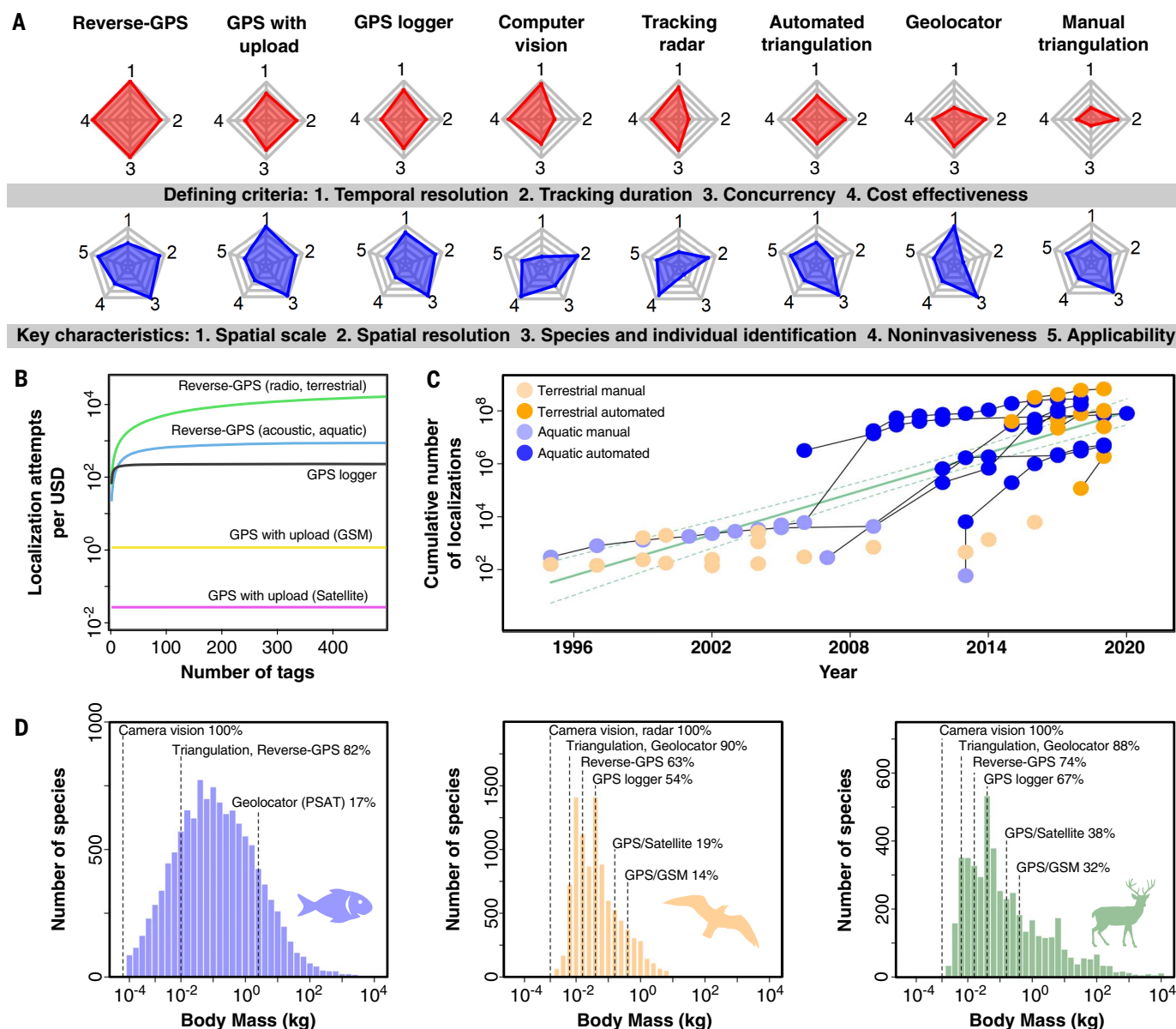


Fig. 1. High-throughput tracking technologies and trends. (A) Qualitative evaluation of the four defining criteria (red) and five key characteristics (blue) of eight major wildlife tracking technologies (ordered according to their high-throughput capacity), as estimated by 23 experts in animal tracking. Higher scores represent more favorable high-throughput performance. (B) Cost-effectiveness was quantitatively estimated as the number of localization attempts per investment (1 US dollar) for five tag-based tracking systems. (C) Pronounced increase (six orders of magnitude) 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, with those linked by black lines representing yields from the same system across years; the mean trend is shown in green with 95% CIs. (D) Proportion of species that can be tracked by the smallest tags currently used to track fish (tag mass <2% of body mass), birds, and mammals (<3% of body mass for both). For details on estimation procedures and data sources, see supplementary materials (101). GSM, global system for mobile communications; PSAT, pop-up satellite archival tags.

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 $\delta t = 1$ to 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 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 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 movie S1). However, the combination of high temporal and low spatial resolution tends toward the opposite bias especially when movement is slow with many stops, owing 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 what was formerly possible (Fig. 1, B and C), 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 on the basis of our four defining criteria and their main limitations and strengths (Fig. 1A), and we quantified their cost-effectiveness as the total number of localizations (the product of the first three criteria that can be generated on the basis of the same investment (Fig. 1B)). These comparisons revealed three fairly distinct groups of high-throughput technologies (see “Data collection” for details): (i) 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 constraints are relatively limited spatial scale and installation costs. (ii) GPS with upload (11, 12, 36–42) and GPS loggers (9, 43–45), also meet most criteria under certain circumstances and can track terrestrial (and some aquatic) animals at large to global scales; however, these are usually less cost-effective and less applicable (expensive tags, cannot be applied under water and are limited to relatively large animals or to study systems where animals, including small ones, can be recaptured to retrieve data). (iii) Tracking radars (46) and computer vision (47–51) also meet most criteria under certain circumstances and are usually noninvasive but are less cost-effective and much more restricted in their applicability, spatial range, and tracking duration; further, 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 covariation patterns and individual fitness (Fig. 2).

Practical difficulties in measuring individual states, traits, and behaviors have restricted researchers to conducting studies under controlled, often captive, conditions. However, 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*; $\delta t = 1$ to 4 hours) (54) and white storks (*Ciconia ciconia*; $\delta t = 5$ min to 12 hours) (55). Further, an experimental field approach was successfully applied to roe deer (*Capreolus capreolus*; $\delta t = 1$ 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 ($\delta t = 1$ to 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 ($\delta t = 9$ 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 ($\delta t = 1$ to 3 min) of northern gannets (*Morus bassanus*) revealed sex-related variation

in foraging timing and duration and habitat selection in some years but not others (44).

Biotic interactions

High-throughput systems provide the means to detect social and other intraspecific interactions among individuals in natural environments through simultaneous tracking of most or all group members (37, 41); such interactions 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 ($\delta t = 1$ s every fourth day), both dominant and subordinate birds were found to 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 interspecific interactions (see summary figure), 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) as well as in the context of predator-prey interactions (59).

Classic concepts in ecology and animal behavior (e.g., 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 ($\delta t = 8$ s) revealed robust spatial partitioning among two adjacent bat colonies that cannot be explained by commonly hypothesized competition, but could emerge from memory and information transfer (34). High-resolution GPS tracking ($\delta t = 0.2$ s) enabled the assessment of how individual pigeons within coordinated flying groups responded 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 $\delta t = 1$ min), implying that the true nature of predator-prey dynamics among fish cannot be detected by lower resolution data of the same sample size (Fig. 3).

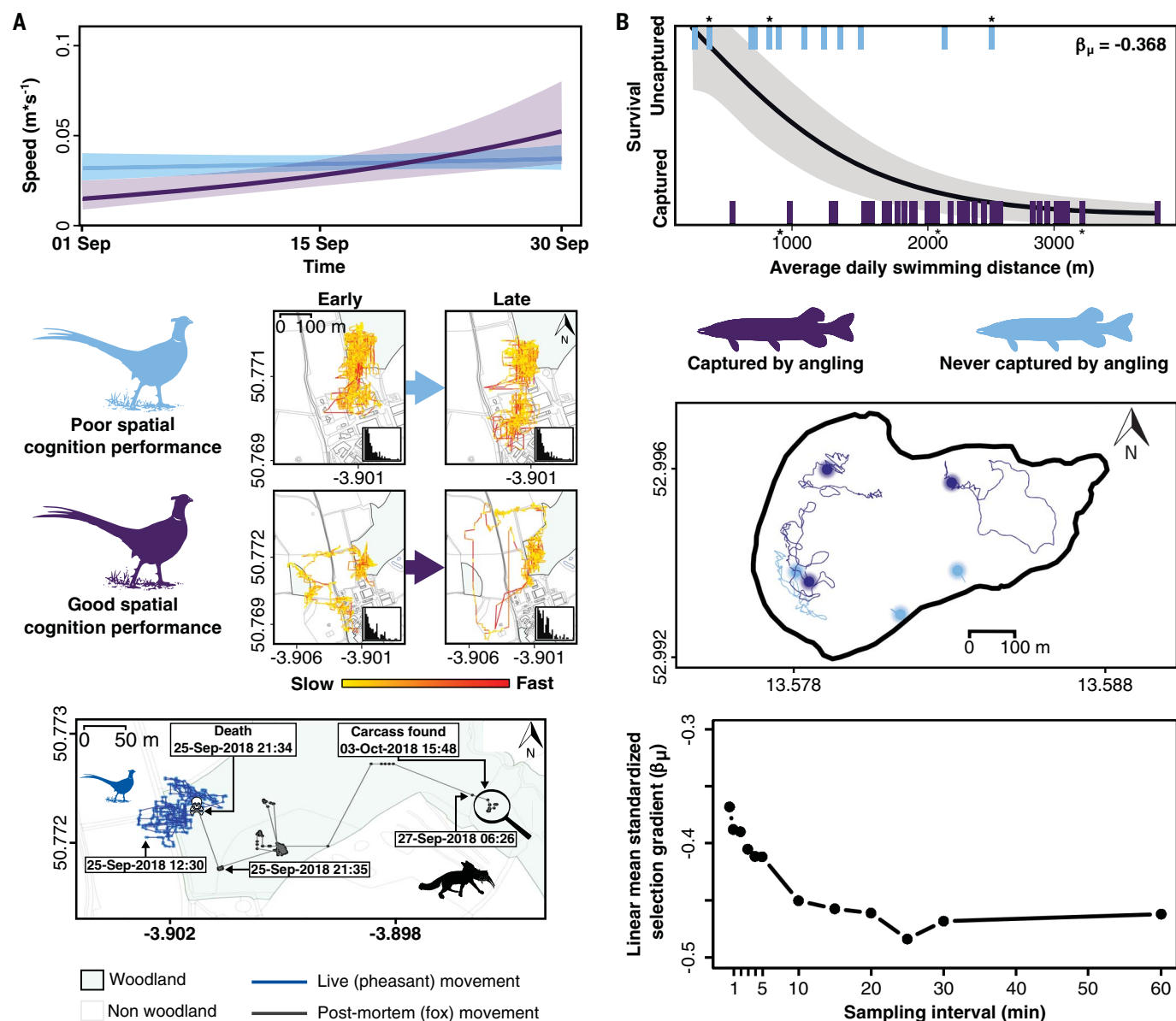


Fig. 2. Inference on patterns of variation in movement, behavior, and fitness among individuals and their potential drivers. (A) ATLAS-tracked ($\delta t = 4$ s) young pheasants (*P. colchicus*) that performed better in spatial cognitive tasks in captivity made slower transitory movements during early stages of exploration in the wild, but their speed increased with experience in 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 (middle plots). Histograms show the number of fast steps (>1 m/s). The bottom map shows the track of a pheasant (blue lines) that was killed and carried away (with the ATLAS tag intact) by an untagged fox (*Vulpes vulpes*) (black lines). 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 (*E. lucius*) tracked in the wild using acoustic trilateration ($\delta t = 9$ 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 noncaptured pike is illustrated in the map by six representative tracks (marked by asterisks in the top plot), with dotted lines representing data gaps ($\delta t > 60$ 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).

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 and movies S3 to S5), providing critical information for developing effective

management and restoration actions (13, 14). For example, high-resolution GPS data ($\delta t = 1$ s) combined with triaxial accelerometry and atmospheric modeling were necessary to reveal differential responses of adult and juvenile griffon vultures (*Gyps fulvus*) to challenging soaring conditions (38) (Fig. 4A and movie S3).

Further, whole-lake acoustic trilateration ($\delta t = 9$ s) revealed interaction between a non-native wels catfish (*Silurus glanis*) and physical features (e.g., water temperature) of a novel environment (27).

High-throughput tracking data, coupled with mapping of relevant human activities,

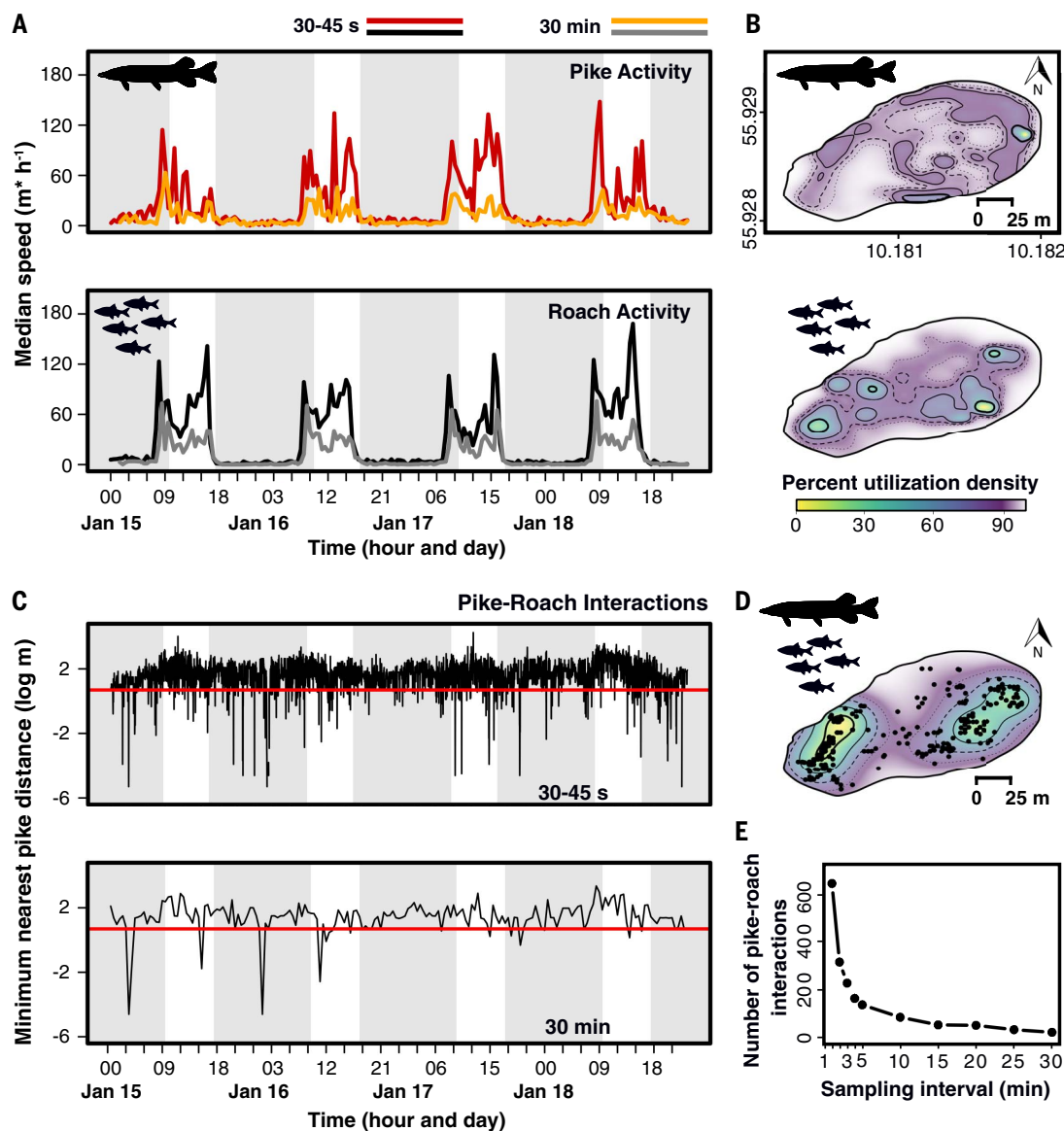


Fig. 3. The nature of biotic interactions. Prey fish (roach, *Rutilus rutilus*, black lines) were tracked using acoustic trilateration ($\delta t = 9$ s) simultaneously with predators (northern pike, *E. lucius*, red lines). Predators and prey were similar in their diurnal cycles (**A**) but differed in their spatial activity patterns (**B**). Short-range (>2 m) predator-prey encounters occurred

throughout all times but more during the night (**C**), and at two large predation hotspots (**D**) that only partially overlapped with the main activity area of the predators. The number of potential predator-prey encounters (**E**) was rapidly underestimated as temporal resolution decreased (longer sampling intervals).

enable evidence-based conservation and management across diverse ecosystems (28). For example, endangered European eels (*Anguilla anguilla*) tracked during downstream migration by acoustic trilateration ($\delta t = 1$ s) showed rapid behavioral shifts 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; see another example in movie S4). This technology ($\delta t = 5$ 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 ($\delta t = 1$ min) and condors ($\delta t = 30$ 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 ($\delta t = 4$ s), for example, showed substantial variation in movement phases at local scales, which remains undetectable even

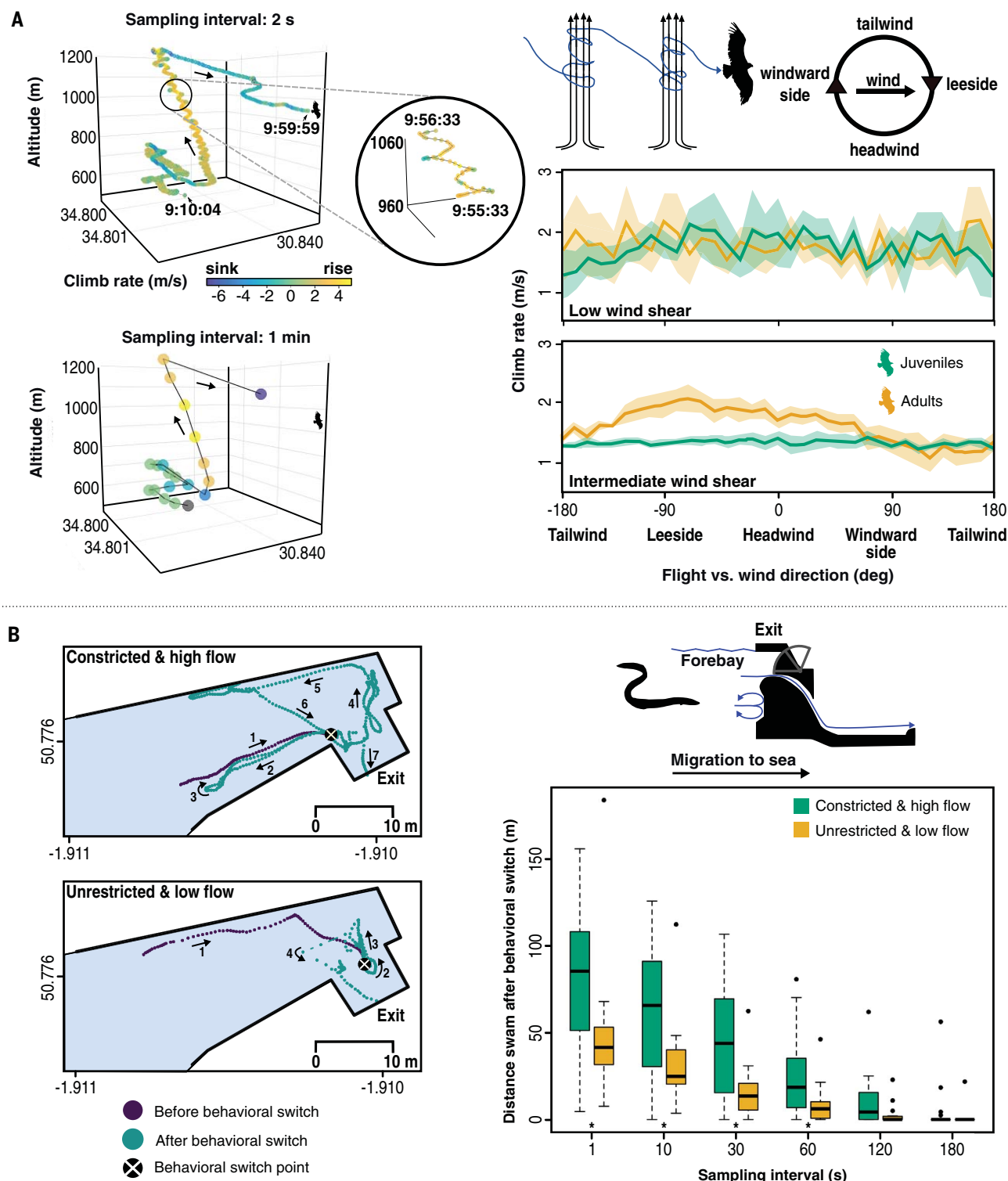


Fig. 4. Insights into the responses of wild animals to their abiotic environment and to human-induced environmental changes. (A) High-resolution ($\delta t = 2$ s) GPS tracking of griffon vultures (*G. fulvus*) revealed that under more challenging soaring conditions (intermediate wind shear), juveniles climbed more slowly in rising-air thermals because of their lower efficiency in circling around wind-drifted thermals compared with adults (38). Vulture thermal circling is clearly evident in the high-resolution data but cannot be recognized even at slightly lower resolution data ($\delta t = 1$ min). According to the Nyquist-Shannon criterion, a typical circling duration of ~ 15 s (~ 4 circles min^{-1} ; zoomed-in section) requires

$\delta t \leq 7.5$ s. **(B)** Acoustic trilateration ($\delta t = 1$ s) revealed that downstream-migrating endangered European eels (*A. anguilla*) shift their behavior from semipassive 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 searches 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.

at slightly lower temporal resolution (Fig. 5). This shows that notions of universal foraging behavior and scale-free movement (68) should be replaced by case- and scale-specific behavior and movement, and that high-resolution data are needed to detect differences among these patterns. Furthermore, high-resolution data enabled researchers to distinguish 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. However averaging could be misleading in nonergodic 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., $\delta t = 1$ hour) (56), high-resolution data are necessary for field experi-

ments involving short-term behaviors, fine-scale encounters, or multiple interacting individuals or 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 nonmanipulated free-ranging individuals. For example, 149 nonmanipulated ATLAS-tracked ($\delta t = 1$ to 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

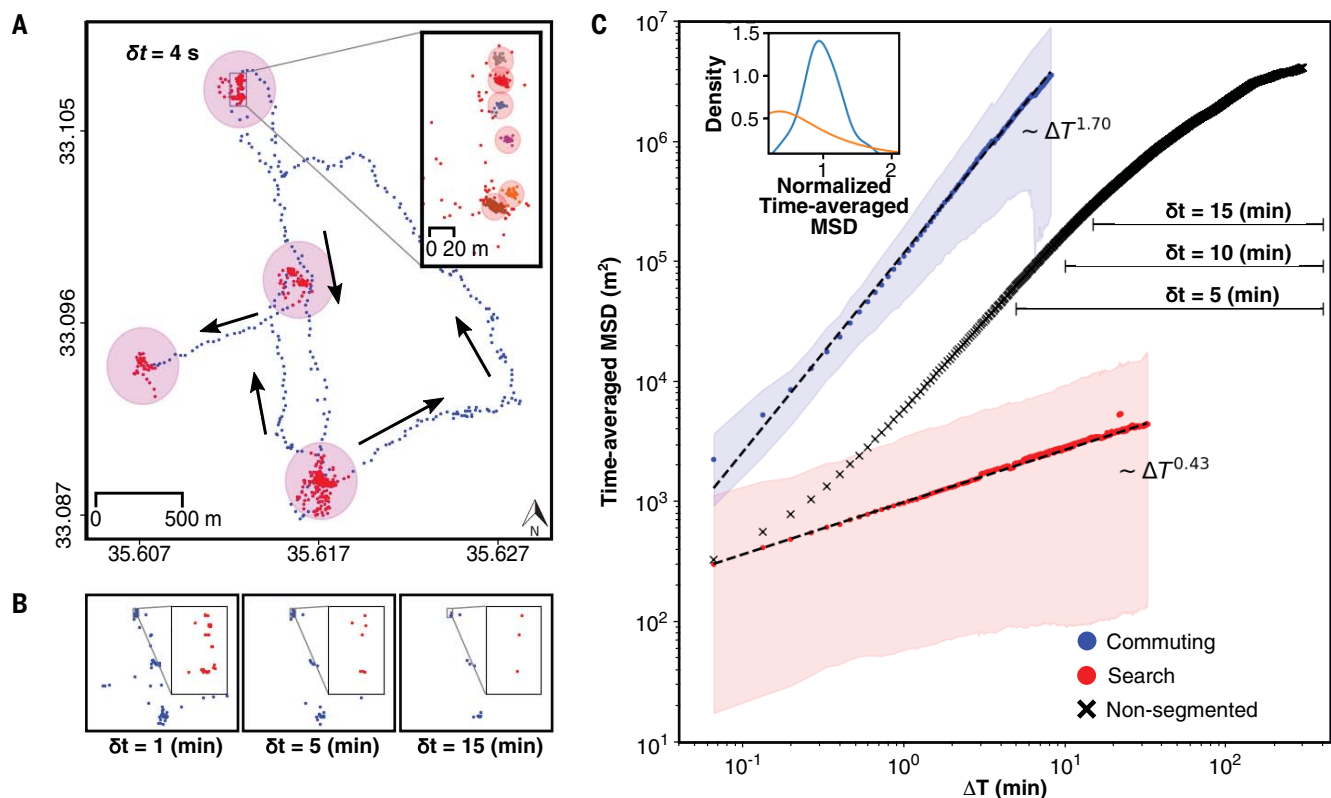
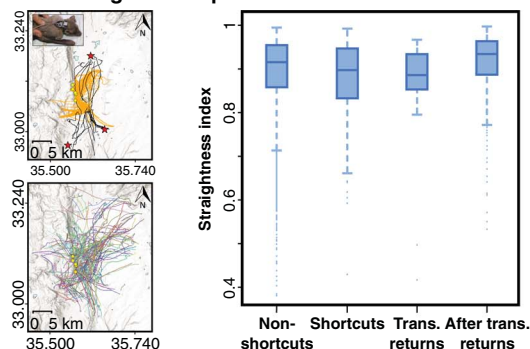


Fig. 5. Detecting commonalities and differences in animal movement and behavior across multiple spatiotemporal scales. Segmentation of a 3.6-hour track of a single black-winged kite (*E. caeruleus*) randomly selected from 155 days of high-resolution ($>10^6$ localizations) ATLAS tracking ($\delta t = 4$ s) revealing (A) four segments of area-restricted search (ARS, red dots within purple circles) connected by commuting flights (blue dots with black arrows showing direction). Zooming into one ARS (inset) reveals six local clusters (orange circles), which cannot be detected using lower-resolution data (B) that entail insufficient information (only 34, 7, and 3 ARS localizations for $\delta t = 1$, 5, and 15 min, respectively), compared with the high-resolution data ($\delta t = 4$ s; 491 localizations). (C) Time-averaged mean square displacement (MSD) of

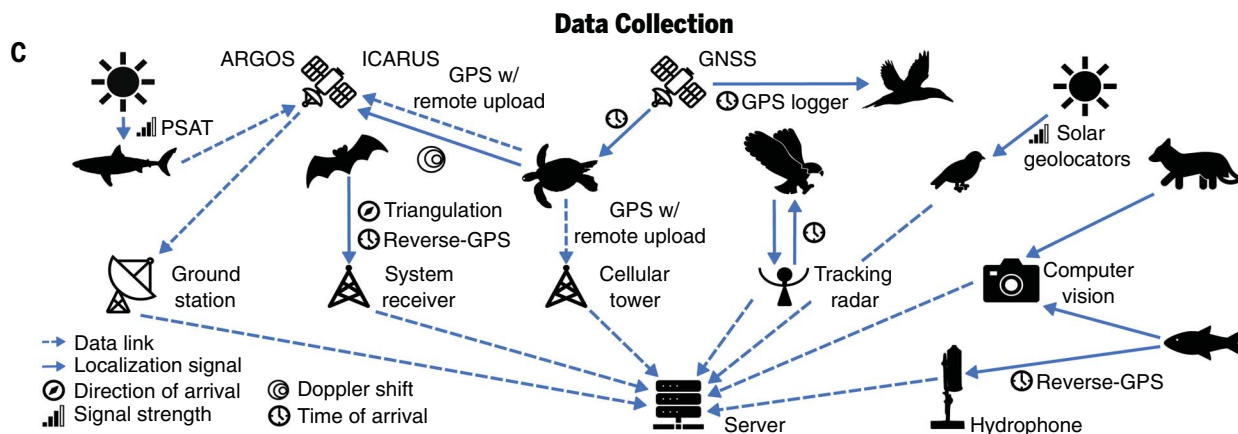
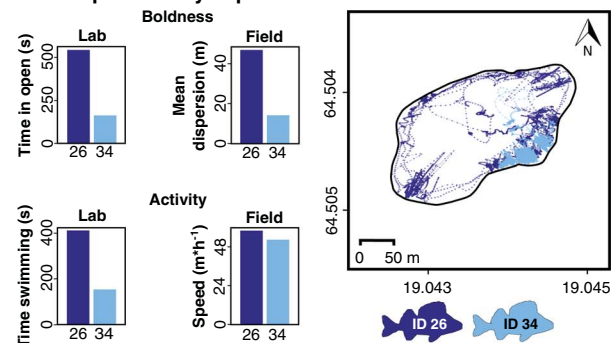
nonsegmented daily tracks recorded across 155 days (black crosses), which is not well fitted to a single power-law exponent across all temporal scales, but has a steeper slope indicating superdiffusive motion at $\Delta T < 100$ min and a shallower slope indicating subdiffusive motion $\Delta T > 100$ min. Segmenting the track to commuting and ARS (blue and red shaded areas, representing 90% of the trajectories), a clear distinction emerges between superdiffusive ergodic commuting (blue) and subdiffusive nonergodic 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 a notably more limited temporal range, as indicated by the bars for $\delta t = 5$, 10, and 15 min.

Study Design

A Animal cognition experiments

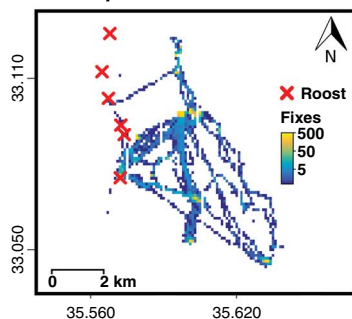


B Animal personality experiments

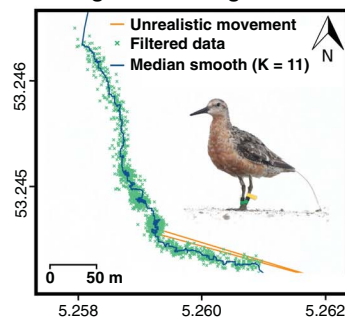


Data Processing

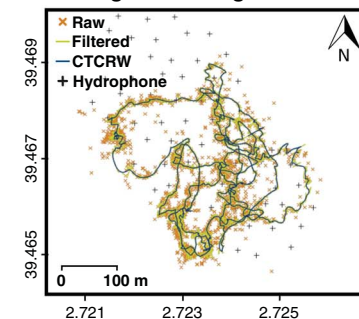
D Data exploration



E Filtering & smoothing

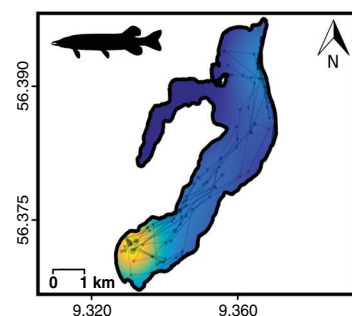


F Filtering & modeling

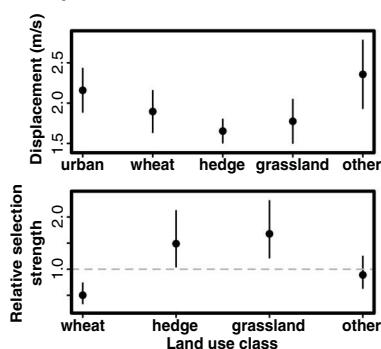


Data Analysis

G Kernel density estimation



H Step selection function



I Hidden Markov modeling

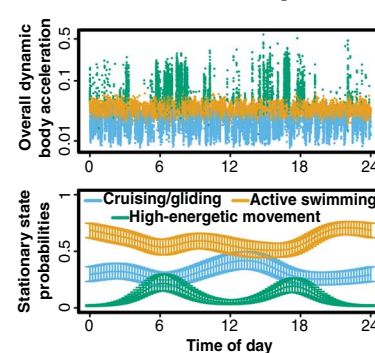


Fig. 6. Key steps in high-throughput movement ecology research. (A) ATLAS-tracked ($\delta t = 1$ to 8 s) Egyptian fruit bats (*R. aegyptiacus*), after being translocated to the periphery of their foraging range, returned to their specific foraging tree along straight trajectories (black lines), similar to nonmanipulated individuals taking shortcuts, altogether complementing field evidence for the existence of a cognitive map (10). (B) Evidence for consistent differences between bolder and more active (purple) versus shy and less active (blue) European perch (*Perca fluviatilis*) as observed in lab trials and after release to the wild. (C) An overview of primary 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, solar, or 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 cellular link; (eagle) radar tracking; (gannet) GPS logger; (small bird) solar geolocators; (fox) computer vision tracking; and (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 ($\delta t = 9$ s) red knots (*Calidris canutus*) and (F) acoustic trilateration tracking ($\delta t = 2$ to 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 by a pike (*E. lucius*) using kernel density smoothing and residence patch analysis; (H) habitat selection assessed by applying integrated step-selection functions to ATLAS data ($\delta t = 8$ 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.

traits can be introduced to novel wild environments, to test predictions on trait-movement associations. For example, ATLAS-tracked ($\delta t = 4$ 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 notable 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, and hence can differ between laboratory and wild conditions (70). Finally, individual states can be manipulated and the outcome in the wild can be monitored to examine long-term consequences of short-term environmental stress. For example, acoustic trilateration ($\delta t = 1$ 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 of these use an electronic animal-borne tag that either transmits a signal (transmitter localization) or receives or senses a signal (receiver-sensor localization), whereas the other two use animals or tags that reflect either an ambient signal (passive reflection) or a signal 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 nontagged 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 primary 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, similar to GPS, these are accurate trilateration-based systems, but unlike GPS, raw data and localizations are collected by the system and not on the tag. Reverse-GPS systems use small, energy-efficient, and inexpensive tags, which can be used to track multiple animals simultaneously at high spatiotemporal resolution (typically $\delta t = 1$ to 10 s, 1 to 5 m median spatial error) and 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) but did not reach high-throughput capacity until after automation during the past decade and even more recently for terrestrial systems (Fig. 1C). Their main limitations are relatively restricted range (≤ 100 km) and installation costs.

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

recapture or tag recollection (9), which further limits spatial coverage and applicability.

Tracking radars use active reflection of radio signals and are capable of collecting extensive movement data of many nontagged animals simultaneously at high spatiotemporal resolution [e.g., $\delta t = 1$ 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 noninvasively (i.e., without trapping and tagging) track wild birds (47) and fish (49, 50, 51) in their natural habitats at very high spatiotemporal resolution (e.g., $\delta t = 0.03$ s). However, camera tracking in the wild is typically limited to short ranges, an individual's identity cannot be 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 ≤ 30 min) or intermittent.

Data processing and analysis

As in other fields, managing, processing, and analyzing massive datasets in a timely manner present major challenges (75). The computing infrastructure needed to store and analyze data is 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, as well as location errors such as outliers (Fig. 6, D and E).

Preprocessing 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—which currently range between 10^6 and 10^9 data points per study for basic movement data alone (Fig. 1C)—to be processed on conventional computing hardware. Use of 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 pack-

ages to aid implementation (2, 82). Further methodological advancements allow identification of how individual foraging attempts are driven by highly dynamic local environments (85), as well as 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 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” (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 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 “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 preprocessing pipelines, and offer valuable opportunities for 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, epidemiology, geography, and social sciences is crucial for advancing movement ecology research and facilitating efficient education and outreach.

Major challenges and future directions

Key high-throughput technologies provide the means to characterize, in fine resolution, what individual animals do in their natural ecological context. Although low-resolution data might potentially provide equivalent information by increasing sample size (e.g., tracking many 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 local and regional spatial scales (currently ≤ 100 km) 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 may remain limited for at least the near future. Projects focusing on larger spatiotemporal scales (11, 55, 67) are inherently confined to low-throughput tracking, with data collected at much lower frequencies 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 (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 for their integration (1, 65). We also call for better integration among high-throughput technologies, especially between reverse-GPS systems and computer vision, to provide detailed information on both tagged and nontagged interacting animals and their environments. Challenges in integrating contemporary tracking technologies—which hinder progress in addressing both small- and large-scale and single- and cross-taxa questions in addition to 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 for elucidating 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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SUPPLEMENTARY MATERIALS

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Supplementary Text

References (102–120)

MDAR Reproducibility Checklist

Movies S1 to S5

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Big-data approaches lead to an increased understanding of the ecology of animal movement

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Animal tracking in a big data world

So-called “big-data” approaches have revolutionized fields of research from astronomy to genetics. Such approaches are not limited to fields that seem inherently technical, because the combination of rapid data collection and advanced analytical techniques could be applied to almost any scientific question. Nathan *et al.* reviewed how these modern approaches are being applied to the very old field of animal tracking and monitoring. Large-scale data collection can reveal details about how animals use their environment and interact with each other that were impossible to explore previously. Such methodological shifts will open new avenues of research—and conservation—across species. —SNV

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