

1 **Big-data approaches enable increased understanding of animal** 2 **movement ecology**

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57 One sentence summary

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

60

61 Abstract

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

74 **BACKGROUND**

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

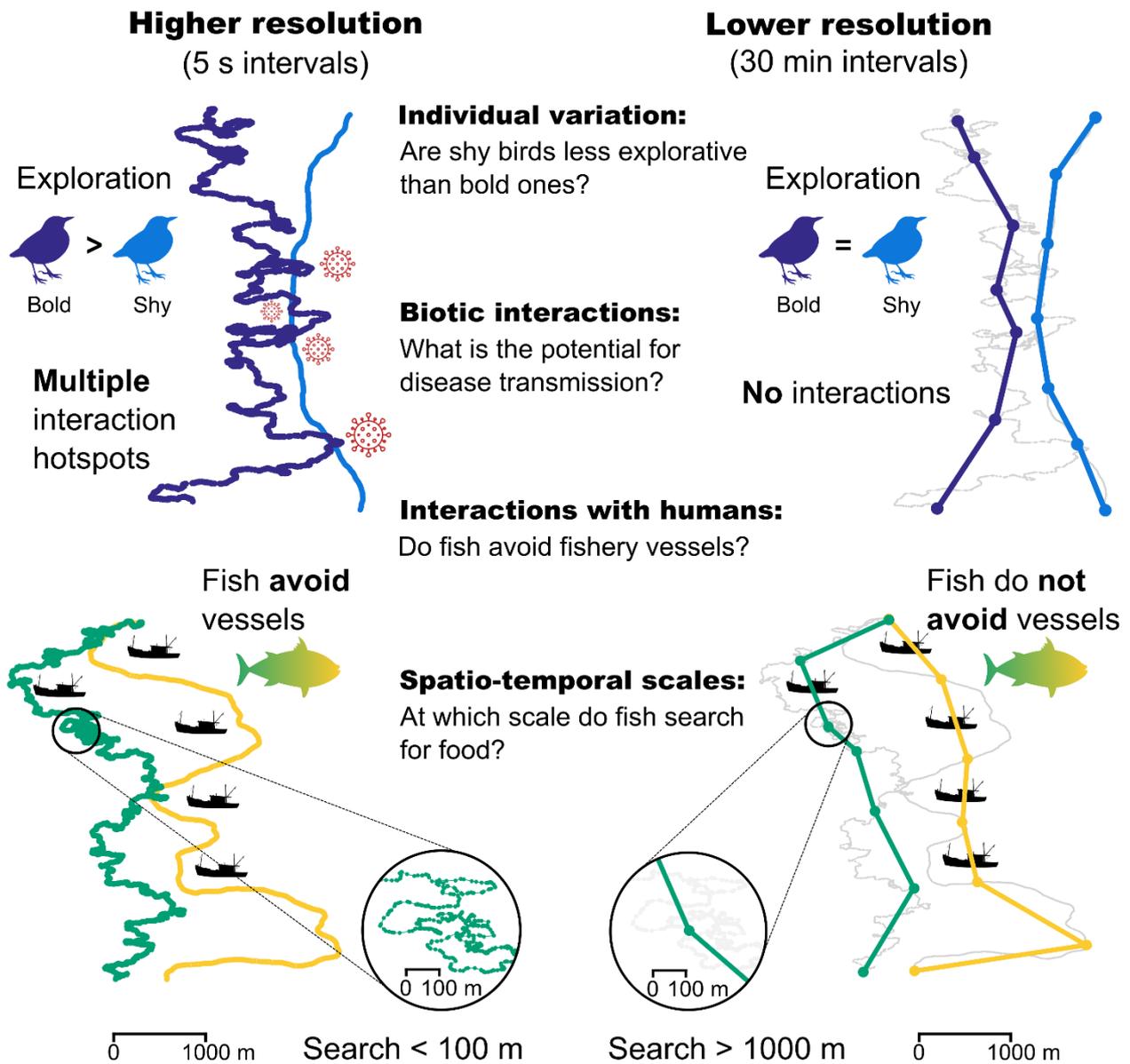
88 **ADVANCES**

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

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

115 **OUTLOOK**

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



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Fig. 0: 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.

143 Main text

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

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

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

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

181 According to the Nyquist–Shannon sampling theorem (16), sampling at time interval δt is
182 sufficient to correctly characterize signals (e.g., behaviors, interactions) that typically last
183 $2\delta t$ or longer. In some of our examples, temporal resolution is around 1Hz ($\delta t=1$ s), enabling
184 characterization of behaviors and interactions lasting just a few seconds. Unfortunately, the
185 phrase “high-resolution” movement data has been used in the movement ecology literature
186 for a wide range of temporal resolutions, with δt spanning seven orders of magnitude, from
187 tenths of a second to several hours and even days. In this review, we (deliberately) narrowed
188 this range down to encompass a much smaller variation (mostly $\delta t=1-10$ s) and report δt for
189 each example. This flexible approach avoids the pitfalls of attempting to find a general
190 standard; rather, research programs in movement ecology should set thresholds for this and
191 the other defining criteria and key characteristics according to the research goals and the
192 key features of the study system (3). Beyond the general trend of increased information loss
193 at lower resolution implied by the Nyquist-Shannon criterion, general best-practice
194 guidelines for selecting δt include, for example, substantial underestimation of the total
195 travel distance (and thereby underestimation of the apparent speed) at relatively low
196 resolution typically applied in movement ecology studies (e.g., $\delta t \geq 30$ min), with stronger
197 bias for more tortuous and faster paths (17, 18; see also Movie S1). However, the combination
198 of high temporal and low spatial resolution tends to the opposite bias, especially when
199 movement is slow with many stops, due to accumulation of errors (18, 19). To alleviate these
200 biases, advanced machine learning methods can be combined with mechanistic agent-based
201 models to capture the relevant resolution and scale of the study system, as we further discuss
202 in the *Data processing and analysis* section.

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

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

226

227 **New big-data frontiers in movement ecology**

228 *Ecology, behavior, ontogeny and fitness of individuals*

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

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

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

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

267 *Biotic interactions*

268 High-throughput systems provide the means to detect social and other intra-specific
269 interactions among individuals in natural environments through simultaneous tracking of
270 most or all group members (37, 41), which have previously been difficult to assess (52; see
271 also Movie S2). For example, in whole flocks of vulturine guineafowl (*Acryllium vulturinum*)
272 tracked by GPS tags ($\delta t=1$ s every fourth day), both dominant and subordinate birds can lead
273 group foraging movements, depending on the resource type being exploited (41). Having
274 more detailed data on the movement of the same number of individuals can also illuminate
275 the true nature of inter-specific interactions (Fig. o), ideally augmented by simultaneous
276 tracking of most or all animals engaged in such interactions (e.g., competitors, predators or
277 prey). This highly challenging need (see *Data collection*) has been acknowledged, for
278 example, in studies of interactions among multiple host, vector and reservoir populations
279 involved in disease transmission (58), and also in the context of predator-prey interactions
280 (59).

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

299 *Interactions with natural and anthropogenic environments*

300 Coupled with fine-scale environmental monitoring, high-throughput tracking systems
301 reveal how animals respond to environmental stimuli (Fig. 4, Movies S3-5), providing
302 critical information for developing effective management and restoration actions (13, 14).
303 For example, high-resolution GPS ($\delta t=1$ s) combined with triaxial accelerometry and
304 atmospheric modeling, were necessary to reveal a differential response of adult and juvenile
305 griffon vultures (*Gyps fulvus*) to challenging soaring conditions (38) (Fig. 4A; Movie S3),
306 and whole-lake acoustic trilateration ($\delta t=9$ s) revealed interactions with physical features
307 (e.g., water temperature) of a novel environment by non-native wels catfish (*Silurus glanis*)
308 (27).

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

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

322 *Patterns and mechanisms across spatiotemporal scales*

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

330 Black-winged kites (*Elanus caeruleus*) tracked using ATLAS ($\delta t=4$ s), for example, showed
331 substantial variation in movement phases at local scales, which remains undetectable even
332 at slightly lower temporal resolution (Fig. 5). This contradicts predictions from the long-
333 debated Lévy flight foraging hypothesis, asserting that animals move in a scale-free manner
334 (68). Importantly, high-resolution data enabled distinguishing ergodic from nonergodic
335 processes, a key question in studies of dynamical systems and stochastic processes that has
336 been overlooked in many disciplines (69), including movement ecology. In ergodic systems,
337 different segments are equally representative of the whole, hence averaging reveals a typical
338 behavior. Yet, averaging could be misleading in non-ergodic systems, which lack a typical
339 behavior. Assessment of ergodicity is therefore crucial in movement ecology, dictating
340 whether one can infer by ensemble-averaging over multiple movement segments. For
341 foraging raptors, ATLAS revealed a substantial distinction between the ergodic,
342 superdiffusive (faster than diffusive) nature of commuting and the nonergodic, subdiffusive
343 (slower than diffusive) nature of local movement, implying a limited number of ways to
344 commute between distant patches but many ways to hunt or stop within a local patch (Fig.
345 5) (35).

346 **The basic steps in high-throughput movement ecology research**

347 *Study design*

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

358 The two approaches can be combined to address key questions in movement ecology
359 through high-resolution tracking of both manipulated and non-manipulated free-ranging
360 individuals. For example, 149 non-manipulated ATLAS-tracked ($\delta t=1-8$ s) Egyptian fruit
361 bats undertook straight shortcuts during their foraging flights, and 23 additional
362 manipulated (transferred to the periphery of their foraging range) bats returned directly to
363 their preferred fruit tree, complementing evidence for a cognitive map (Fig. 6A) (10).
364 Similarly, an individual’s movement before, during and after an experimental trigger can be
365 compared (23) (Fig. 4B). Additionally, individuals with known traits can be introduced to
366 novel wild environments, to test predictions on trait-movement associations. For example,
367 ATLAS-tracked ($\delta t=4$ s) juvenile pheasants that exhibited higher spatial cognition under
368 controlled conditions were slower to explore their landscape shortly after release into the
369 wild but showed significant improvement after a few weeks (32) (Fig. 2A). Although
370 behavioral and cognitive traits measured in confined controlled versus wild conditions
371 might be similar (e.g., Fig. 6B), trait expression, variability, and among-trait correlations are
372 extremely context-dependent, differing between laboratory and wild conditions (70).
373 Finally, individual states can be manipulated and the outcome in the wild monitored to
374 examine long-term consequences of short-term environmental stress. For example, acoustic
375 trilateration ($\delta t=1$ min) of largemouth bass (*Micropterus salmoides*) in a lake revealed both
376 a short-term (first few days) response to experimentally induced stress of increased activity,
377 and unexpected long-term (multiple months) carry-over effects rendering stressed fish
378 vulnerable to hypoxia in winter (21).

379 *Data collection*

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

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

389 The five high-throughput wildlife tracking technologies (Fig. 1) differ in their compliance
390 with high-throughput criteria. Reverse-GPS systems are transmitter localization systems
391 that track transmitting tags through an array of receivers by time-of-arrival estimation
392 (trilateration). The term “reverse-GPS” emphasizes that like GPS, these are accurate
393 trilateration-based systems, but unlike GPS, raw data and localizations are collected by the
394 system, not on the tag. They use small, energy-efficient and inexpensive tags, which can be
395 used to track multiple animals simultaneously at high spatiotemporal resolution (typically
396 $\delta t=1-10$ s, 1-5 m median spatial error) hence regularly provide high-throughput data. These
397 systems include acoustic trilateration of aquatic animals (21-30) and radio trilateration of
398 terrestrial animals (e.g., ATLAS; 10, 20, 31-35). Historically, reverse-GPS techniques were
399 applied to track wildlife >50 years ago (71, 72), yet reached high-throughput capacity only
400 following automation during the last decade, and even more recently for terrestrial systems
401 (Fig. 1C). Their main limitations are relatively restricted range (up to 100 km wide) and high
402 installation costs.

403 GPS and GPS-like systems are receiver localization systems that track tags by trilateration
404 using a satellite constellation. GPS systems with upload retrieve data from tags via a satellite
405 or a cellular link, allowing global coverage at a low-resolution mode (typically $\delta t=15$ min to
406 1 day) and regional coverage (a few hundred km) at high-resolution mode (e.g., 11, 12, 36,
407 37-40). Yet, GPS tags are expensive and relatively heavy as satellite/cellular links and
408 onboard localization calculations impose energy costs, limiting these heavier tags to larger
409 animals (though less so with solar charging) and reducing cost-effectiveness. GPS loggers
410 lacking remote upload facilitate collection of high-resolution data ($\delta=0.1-1$ s) from additional
411 sensors (e.g., accelerometers), useful for estimating energy expenditure, identifying
412 behaviors (73) and neighbors (43), and further refining path resolution through dead
413 reckoning (74). Yet, they require animal recapture or tag recollection (9), further limiting
414 spatial coverage and applicability.

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

426 *Data processing and analysis*

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

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

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

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

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

483 genetic algorithms, initial candidate rulesets for individual decision-making can evolve into
484 a robust ruleset that is able to reproduce the unique range and quality of spatial and
485 temporal patterns in high-throughput data ('reinforcement learning', sensu 89). Such
486 patterns can be revealed by applying machine-learning methods including neural networks
487 and deep learning (90). The combination of multiple patterns in high-throughput datasets
488 at different hierarchical levels and scales leads to an unprecedented model robustness,
489 optimized model complexity and reduced uncertainty (91). In this pattern-driven process,
490 model specification, calibration and validation steps are all implemented dynamically and
491 iteratively during the model runtime thus enabling a 'learning on the go' (89). Overall, the
492 increased availability of high-throughput data will continue to motivate the uptake,
493 refinement and development of novel methods for both data processing and analysis (3, 84,
494 86, 87, 92).

495 *Collaborative networks*

496 By permitting comparisons of animal movement across sites, times, and species, high-
497 throughput technologies can motivate large collaborative networks to address questions on
498 animal adaptations and plastic responses to climate and other environmental changes.
499 Notable examples include the Ocean Tracking Network (93), the European Tracking
500 Network (94), and the Arctic Animal Movement Archive (95). Such collaborative networks
501 and platforms guide the process of establishment and maintenance of tracking
502 infrastructure, facilitate efficient exchange of data, knowledge, analytical tools, software
503 packages and pre-processing pipelines, and offer valuable opportunities in scaling-up study
504 areas, addressing broader ecological questions, training, outreach and funding acquisition
505 (75, 96). Enhanced cooperation among traditionally separate disciplines such as ecology,
506 computer science, engineering, bioinformatics, statistical physics, geography and social
507 sciences is crucial for advancing the field, and to facilitate efficient education and outreach.

508

509 **Major challenges and future directions**

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

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

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685 on Dryad upon acceptance.

686 List of Supplementary Materials:

687 **Supplementary Text for Figure 1**

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

689 **Movie S1**

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

693

694 **Movie S2**

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

698 **Movie S3**

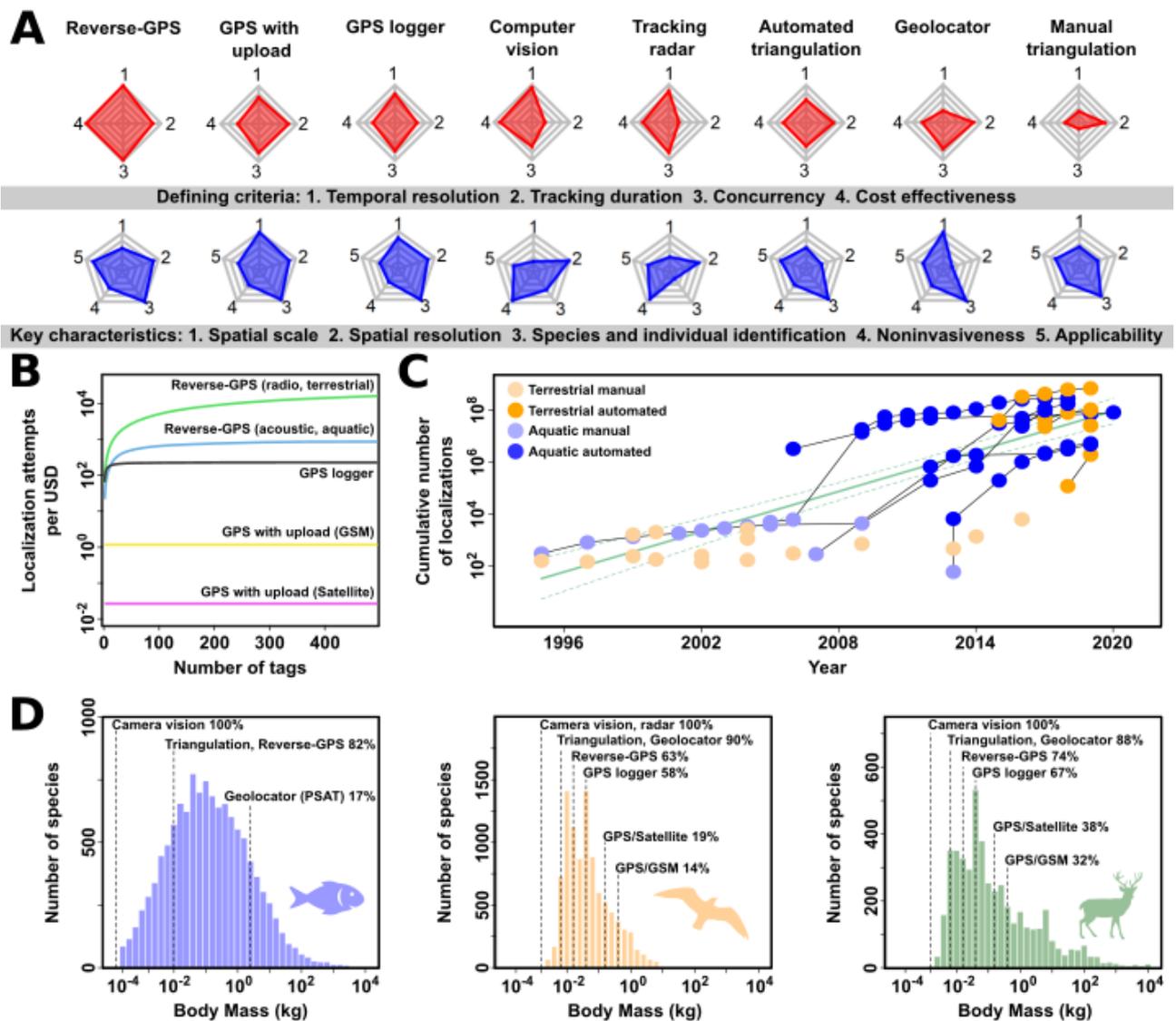
699 High-resolution GPS tracks of three Griffon vultures (*Gyps fulvus*) climbing thermals, illustrating
700 that HTME can provide highly detailed information on animal behavior, which can be used to assess
701 differential age-dependent responses to fine-scale variation in environmental factors.

702 **Movie S4**

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

706 **Movie S5**

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



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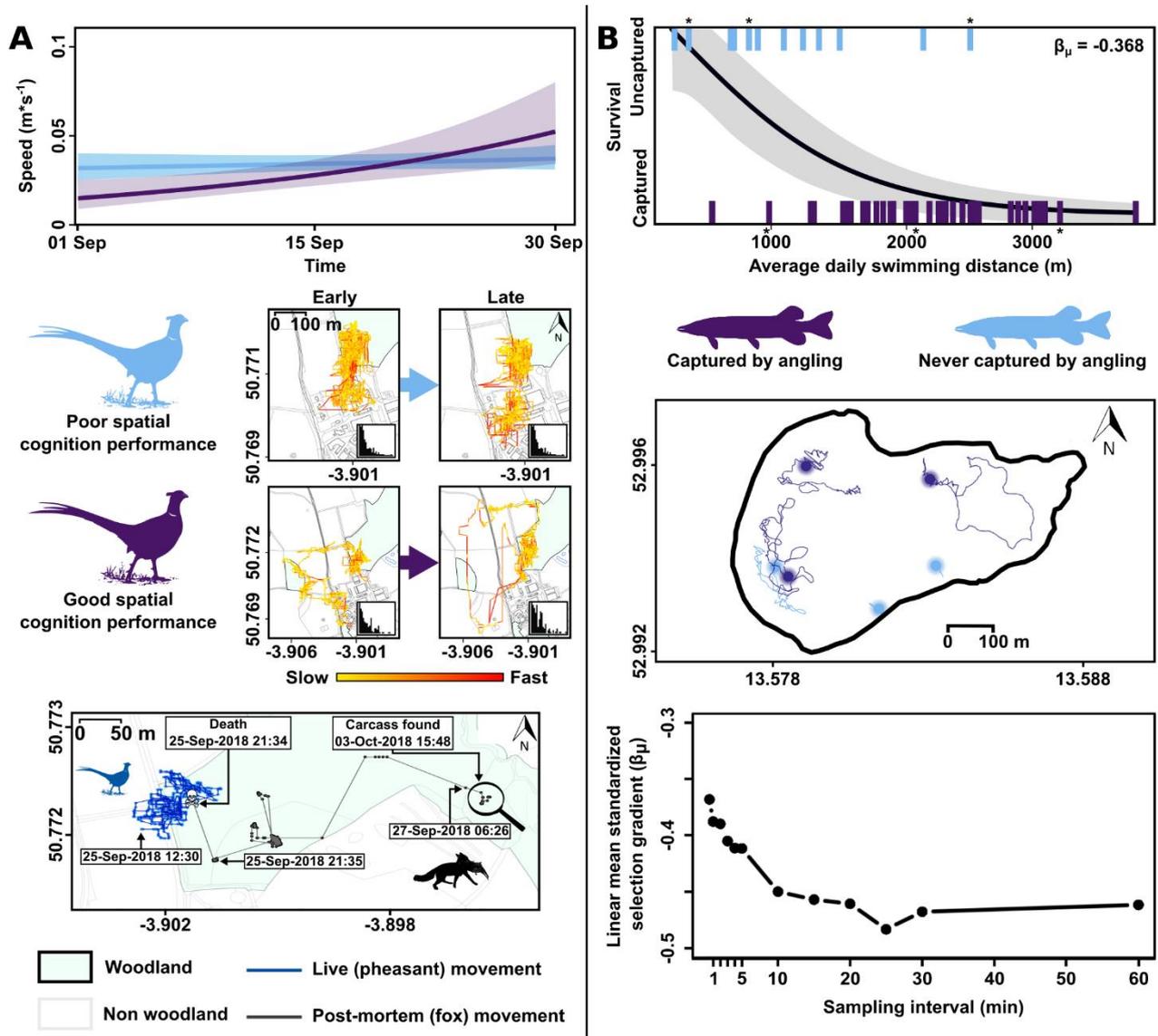
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Fig. 1. High-throughput tracking technologies and trends. (A) Qualitative evaluation of the four defining criteria (red) and five key characteristics (blue) of eight major wildlife tracking technologies (ordered by their high-throughput capacity), 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).



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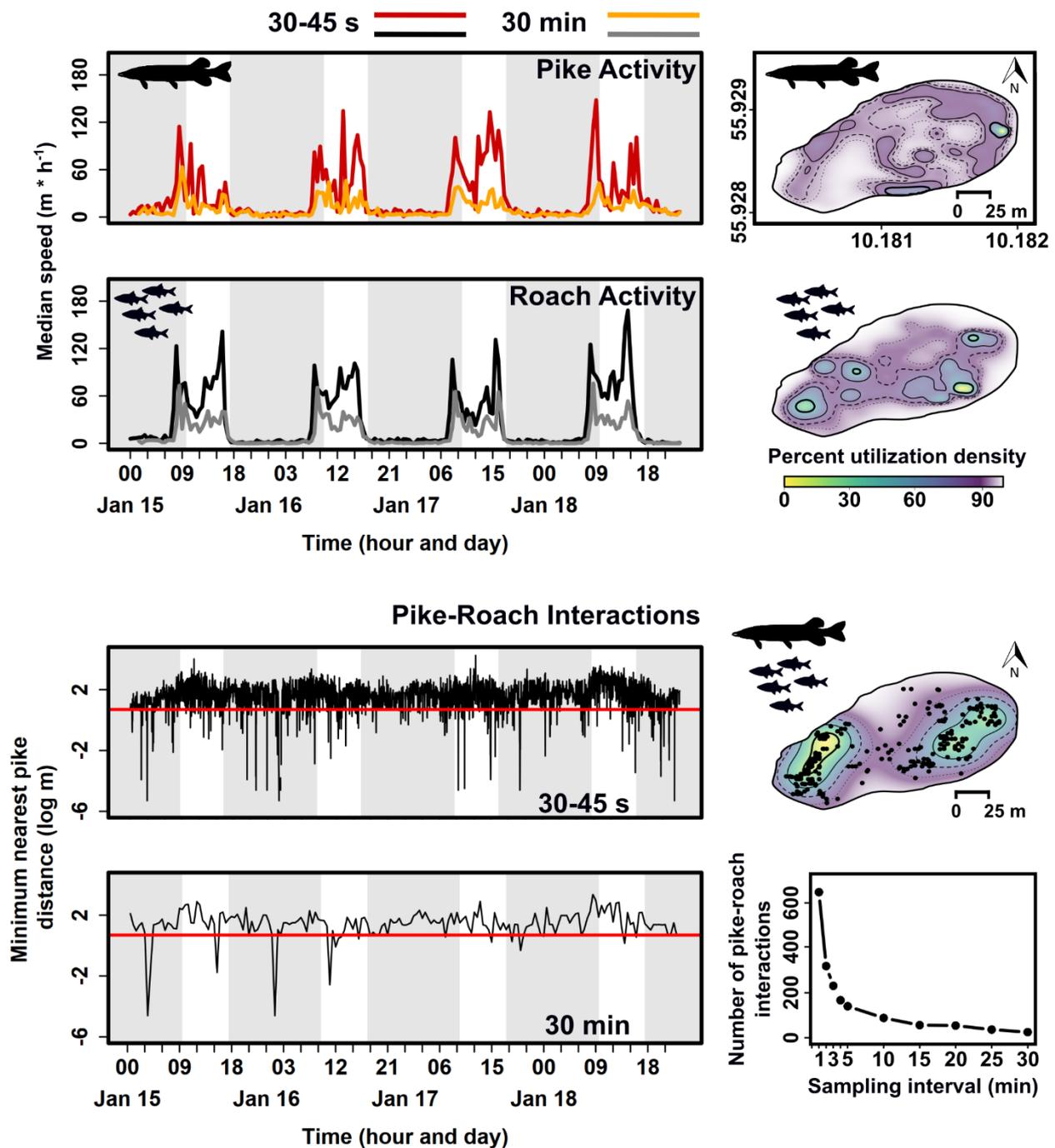
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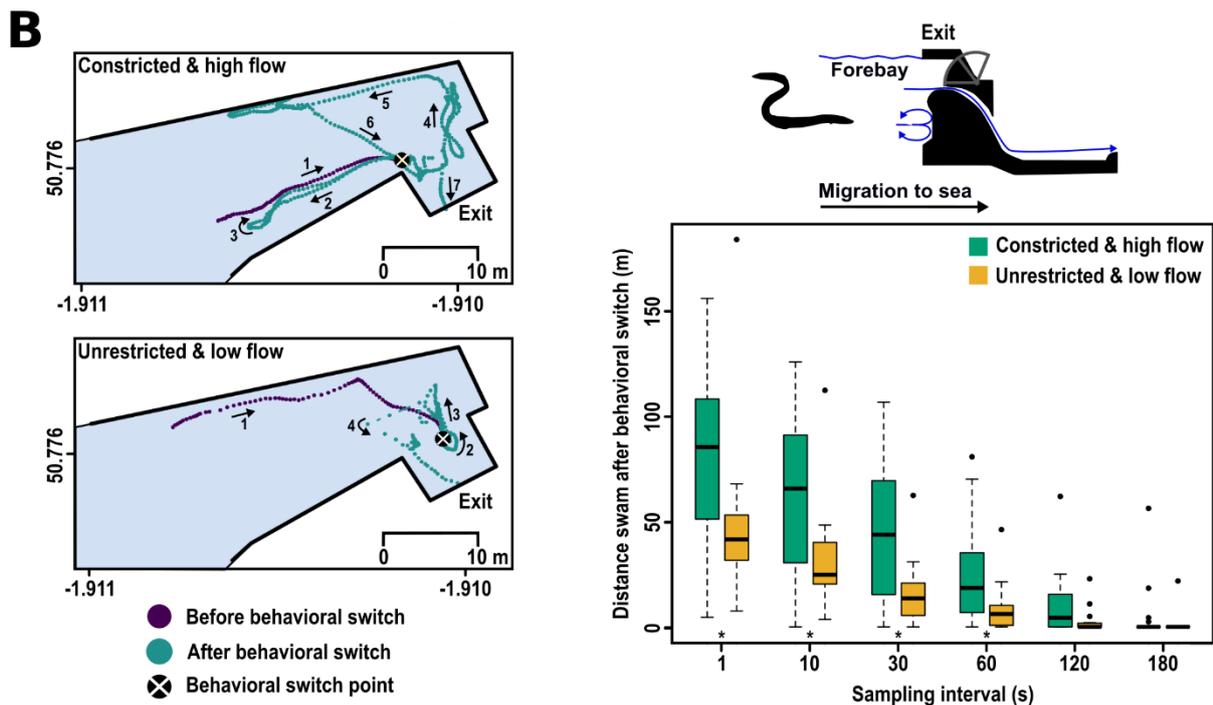
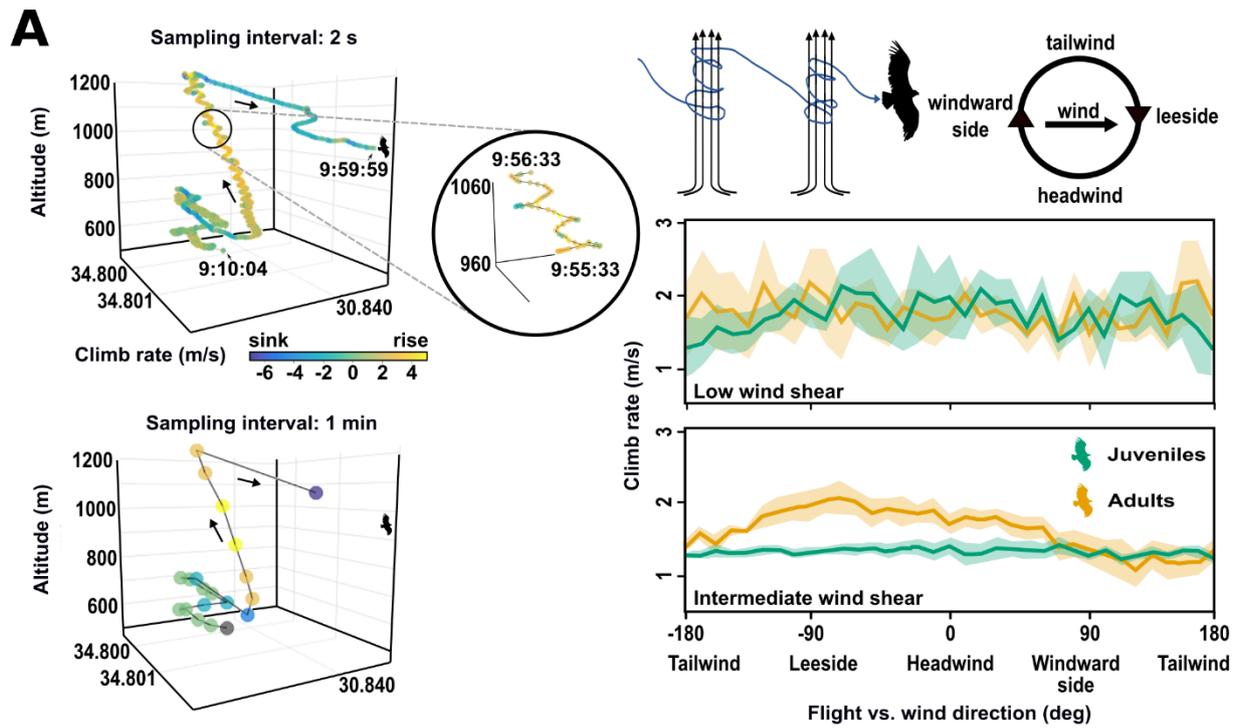
Fig. 2. Inference on patterns of variation in movement, behavior and fitness among individuals, and their potential drivers. (A) ATLAS-tracked ($\delta t=4$ s) young pheasants (*Phasianus colchicus*) that performed better in spatial cognitive tasks in captivity made slower transitory movements during 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 ($\delta t=9$ s) were more likely to be captured by angling (purple) (top plot), suggesting that angling

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



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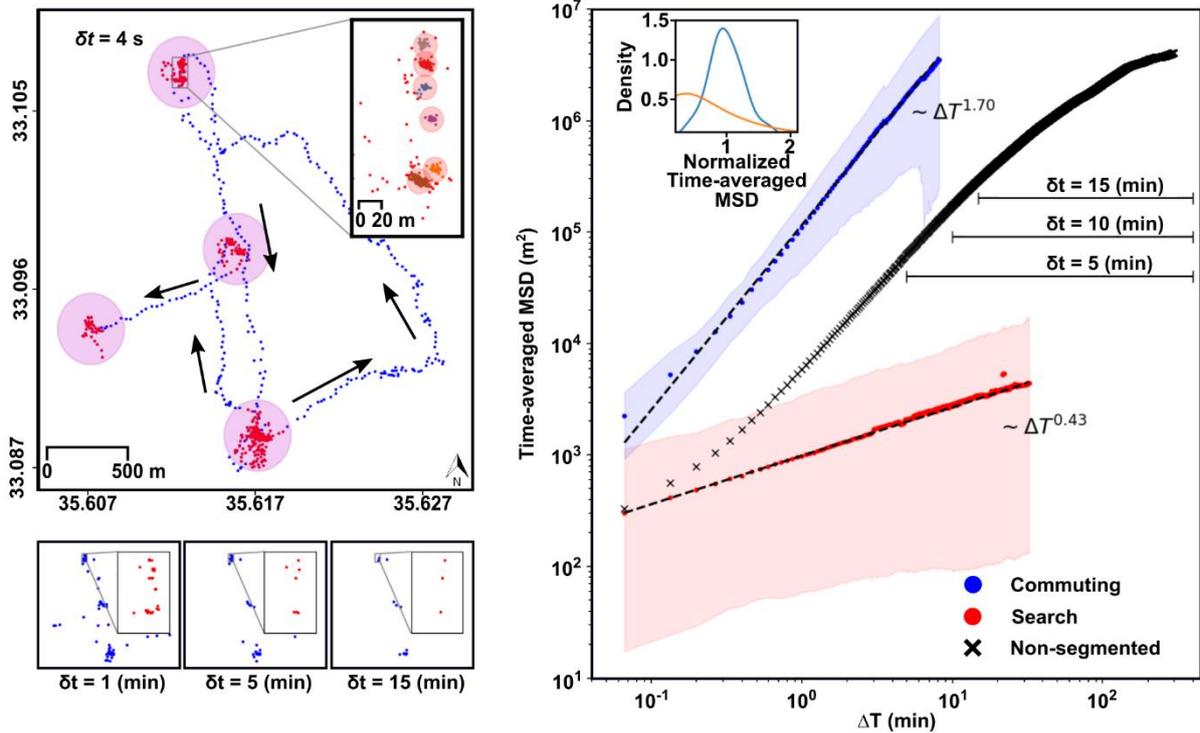
746 **Fig. 3. The nature of biotic interactions.** Prey fish (roach, *Rutilus rutilus*, black) were
 747 tracked using acoustic trilateration ($\delta t=9$ s) simultaneously with predators (northern pike,
 748 *Esox lucius*, red). Predators and prey were similar in their diurnal cycles (top plots), but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



754

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

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



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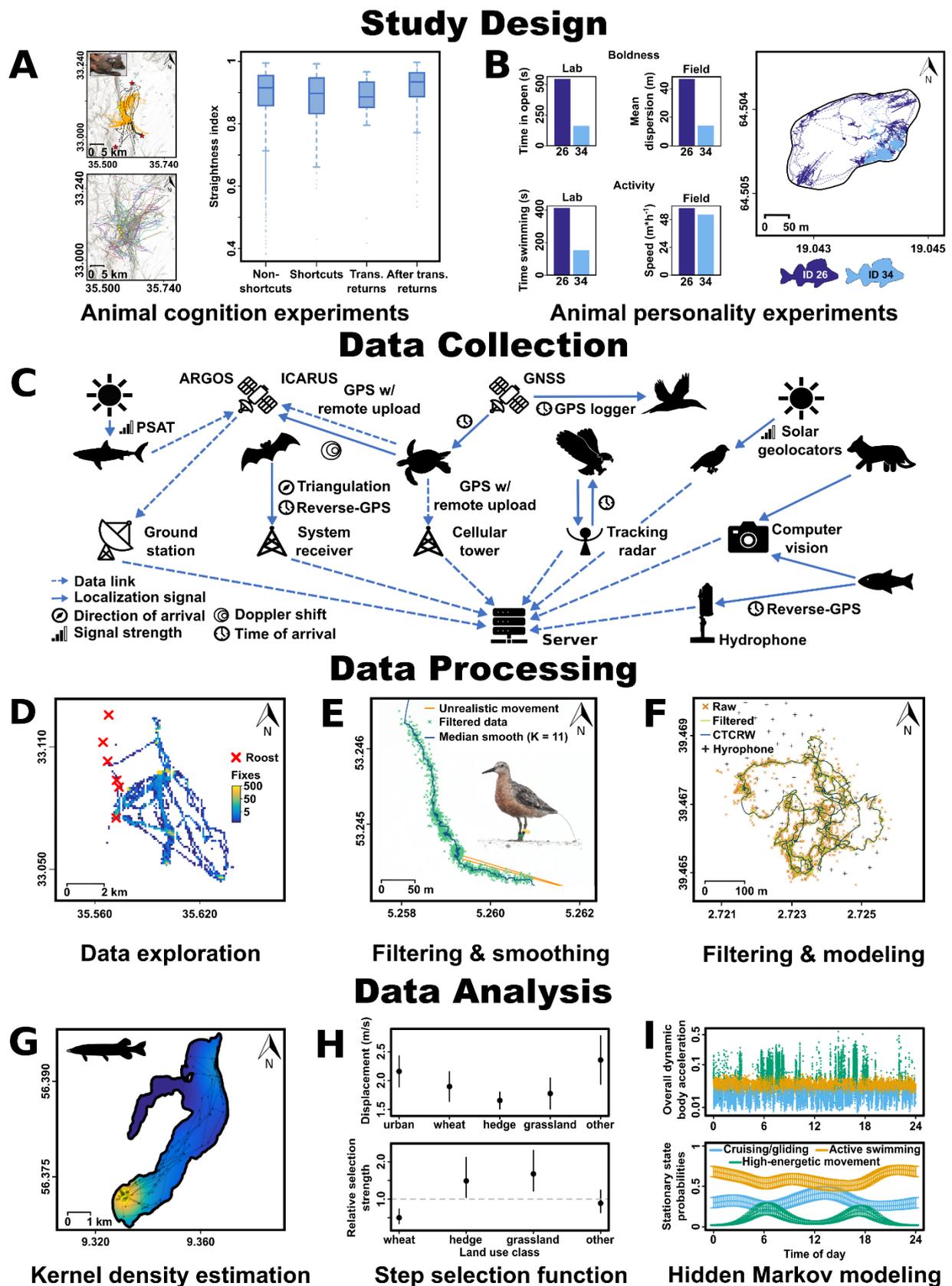
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Fig. 5. Detecting commonalities and differences in animal movement and behavior across multiple spatiotemporal scales. Segmentation of a 3.6-hour track of a single black-winged kite (*Elanus caeruleus*) – randomly selected from 155 days of high-resolution ($>10^6$ localizations) ATLAS tracking ($\delta t=4$ 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 $\delta t=1, 5$ and 15 min, respectively), compared to the high-resolution data ($\delta t=4$ 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 $\Delta T < 100$ min and subdiffusive at $\Delta T > 100$ 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.



791

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

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