Ecology & Evolution

Opinion

Maximizing biological insights from instruments attached to animals

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Instruments attached to animals ('biologgers') have facilitated extensive discoveries about the patterns, causes, and consequences of animal behavior. Here, we present examples of how biologging can deepen our fundamental understanding of ecosystems and our applied understanding of global change impacts by enabling tests of ecological theory. Applying the iterative process of science to biologging has enabled a diverse set of insights, including social and experiential learning in longdistance migrants, statedependent risk aversion in foraging predators, and resource abundance driving movement across taxa. Now, biologging is poised to tackle questions and refine ecological theories at increasing levels of complexity by integrating measurements from numerous individuals, merging datasets from multiple species and their environments, and spanning disciplines, including physiology, behavior and demography.

Testing and refining ecological theories with biologgers

A holistic understanding of complex ecological processes requires creative solutions for collecting data across sites, species, and systems. Archival or transmitting instruments attached to animals (hereafter, biologgers) (see Glossary) have become routine tools for recording physiological, behavioral, and demographic characteristics of individuals, and for inferring their interactions with environmental and ecological features [1] (Figure 1). These animal and ecosystem insights are obtained through various levels of data processing by the researcher, ranging from minimal (sensors that measure heart rates and ambient light levels) to extensive (calculations of activity budgets and energy expenditure from sensor measurements) (Figure 1 and see Table Sl in the supplemental information online). The resulting discoveries in animal physiology, ecology, and evolution span temporal and spatial extents and resolutions that far exceed those possible from traditional observation and mark—recapture approaches. Major discoveries include understanding how navigation abilities allow animals to migrate across the globe and how physiological and anatomical adaptations allow animals to inhabit harsh regions such as polar and deep-ocean habitats.

The rapid development of biologging has motivated numerous proposals for future directions. The biologging community has been urged to integrate with other disciplines [2], use mathematics and optimality [3], re-unite big data approaches with field-based ecological processes [4], target key knowledge gaps [5], learn lessons from human mobility research and reconnect tools and questions [7,8]. In recent years, biologging studies have transitioned from describing unique biological observations to adopting a more rigorous scientific

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Highlights

Many animal characteristics that strongly influence population, community, and ecosystem dynamics are difficult or impossible to measure using traditional field methods.

Biologging sensors enable broad-scale, high-resolution measurements of the physiological, behavioral, demographic, social, and environmental interactions underpinning patterns in nature.

We present a framework, case studies, and outstanding questions for integrating biologging data with theoretical concepts to facilitate process explanation and prediction.

Future studies should use biologging technology to rigorously test ecological hypotheses, transitioning from pattern description to refining and advancing ecological theory.

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approach. Now, researchers typically formulate defined questions, ensure adequate sample sizes,

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nighttime foraging hours to sleep in the safety of darkness (Figure 2) [23]. More broadly, this research provides insights into

and conduct in-depth analyses, shifting from simple movement descriptions to hypothesis-driven investigations. Biologging studies have also applied 'big-data' approaches to tackle behavioral and ecological mechanisms underlying animal movement and the proximate internal and external factors that constrain them [9,10]. In turn, the discoveries and natural history descriptions enabled by biologging technology are primed for testing and refining long-standing ecological theories [11], with implications for broad generalizations [12] and evidence-based conservation solutions [13].

We believe a critical next step is to use biologging to answer questions that span multiple taxa, such as whether generalizable 'rules' underpin complex movements and species interactions [14]. For many emerging questions, ecological theory exists to generate hypotheses about how animals behave, and how behavior scales up to shape species' distributions and broader ecosystem processes [15]. In contrast to controlled laboratory experiments, biologging facilitates measurements in natural settings where competing selective pressures such as predation, starvation, competition, and infection exist. For example, data from satellite trackers and accelerometers can be used to estimate foraging rates and prey densities to test hypotheses about functional responses (i.e., the shape of the curve that describes prey capture rates by predators as a function of prey availability) (Figure 1). We illustrate the potential of data from biologgers to integrate complex data into mechanistic evaluations, thereby offering a powerful approach to hypothesis testing and theory refinement.

Examples of development from discovery to theory

We provide three case-studies that range from single-species behavioral research to multispecies interactions and consequences for population dynamics (Figure 2). In these examples, we highlight the progression from pattern description to hypothesis testing to theory development and suggest directions for future research.

State-dependent risk-taking throughout oceanic foraging in elephant seals

Body condition is hypothesized to mediate how animals navigate risk—reward trade-offs; however, the difficulty of simultaneously measuring body condition, predation risk, and food rewards in the wild has limited our understanding of how intrinsic states affect risk-taking behavior [16]. Biologgers have begun to address this gap by collecting data on animal movement behavior. For instance,

timedepth recorders facilitated the discovery that northern elephant seals (Mirounga angustirostris) cease swimming and passively drift during some dives [17]. The discovery of these so-called 'drift dives' led to the hypothesis that seals in inferior body condition with less body fat would sink faster [18J. Later, this hypothesis was tested with longitudinal energy gain rates [19], enabling drift dives to be used as a valuable metric for estimating body composition [20] at fine spatiotemporal scales throughout oceanic foraging trips. In addition, measurements of drifting seals were used to test hypotheses about the functions of drift dives for resting and food processing [21,22J. Finally, drift dive analysis provided a method to estimate daily body composition and time—activity budgets throughout months-long oceanic foraging trips, which enabled the testing of predictions from statedependent risk-taking theory regarding optimal periods for animals to rest and forage [23J. This three-decade research arc, examining whether behavior is state-dependent throughout oceanic foraging trips, demonstrated that seals in superior body condition sacrifice more profitable how other wild animals may move relative to ambient light levels, particularly in marine environments where light levels are mediated by depth in

addition to location and time-ofday.

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Developing new technologies and analytical approaches enables the study of state-dependent behavior in free-ranging animals. New on-board processing algorithms have been developed to estimate and transmit real-time body composition data to test state-dependent behavior in marine species that do not perform drift dives [24]. Likewise, other components of an animal's internal state (e.g., hunger, heat, stress, and exhaustion [25]) may influence behavior and could be measured with new sensors. In the future, state-of-the-art physiological biologgers that measure brain activity [26] and heart rate [27] could be used to test theories of physiological recharge, rebound, and replenishment (e.g., sleep quotas) in other species [28]. Additionally, simultaneously instrumenting predators and prey across dynamic conditions [29-31J, which has been achieved in some study systems, could be used to test theoretical predictions of dynamic landscapes of fear or energy landscapes frameworks.

Social and experiential learning in whooping cranes

Understanding how animals learn long-distance migrations has implications for wildlife conservation and management, including the likely success of protected area designation and species reintroductions or translocations. The role of social versus experiential learning in migratory behavior has been tested in studies of reintroduced whooping cranes (Grus americana) (Figure 2) . Using satellite transmitters and very high frequency (VHF) radio telemetry tags, the movements and survival of re-introduced cranes demonstrated successful migration and dispersal patterns [32] and motivated hypothesis testing about whether reintroduced cranes migrate more efficiently when flying with experienced birds [33]. A long-term satellite tracking dataset indicated an ontogenetic switch from social to experiential learning as

birds age, allowing them to track resources throughout their migration at all ages [34]. This work transitioned from initial descriptive discoveries (examining whether reintroduction was a successful management strategy) to theory-testing (disentangling the roles of social versus experiential learning).

Future biologging research could provide answers to many remaining questions pertaining to animal learning and social interactions. For example, biologgers could help resolve the populationlevel consequences of interrupted information transfer (e.g., by human-made noise) in systems where social learning is a primary mechanism shaping movement strategies [35]. Likewise, many facets of information gathering, particularly social cues and eavesdropping on other species, remain poorly understood but could be answered with animal-borne microphones or video recorders [36,37].

Migration based on past and current resource availability across species

Foundational biologging discoveries about memory and behavioral compensation have set the stage for rich theory and emerging tools to address long-standing questions about migration [38]. One area that has seen significant theoretical progress across species and systems is the influence of variation in resource availability on migratory behavior (Figure 2). In the late 1970s, researchers observed simultaneous changes in plant phenology and migratory movements in waterfowl [39]. Later, biologgers were used to examine the link between vegetation green-up and ungulate migration decisions [40]. Follow-up studies tested hypotheses that mule deer (Odocoileus hemionus) migrate in concert with green-up, maximizing the intake of high-quality forage along migration routes [41], and that the rate and order of green-up influences the ability of animals to green-wave surf [42]. Simulation of zebra (Equus burchelli antiquorum) and mule deer movement, and empirical validation with GPS tracks, showed that previous experience (memory) of green-up patterns also plays an essential role in migration [43,44]. More recently, biologging data has been used to suggest revising movement theory to include the roles of memory [45] and social cues [37] alongside the traditional drivers of contemporaneous environmental conditions perceived by individuals.

Glossary

Behavioral compensation: animals change their behavior to overcome constraints (e.g., regulating life history timing or transit speed to reach a destination on-time or match presence with resource availability peaks). Biologgers: instruments attached to animals that record and/or transmit physiological, behavioral, and demographic characteristics of individuals, and their interactions with environmental and ecological features. Dynamic landscapes of fear: spatial and temporal variation in prey perception of predation risk.
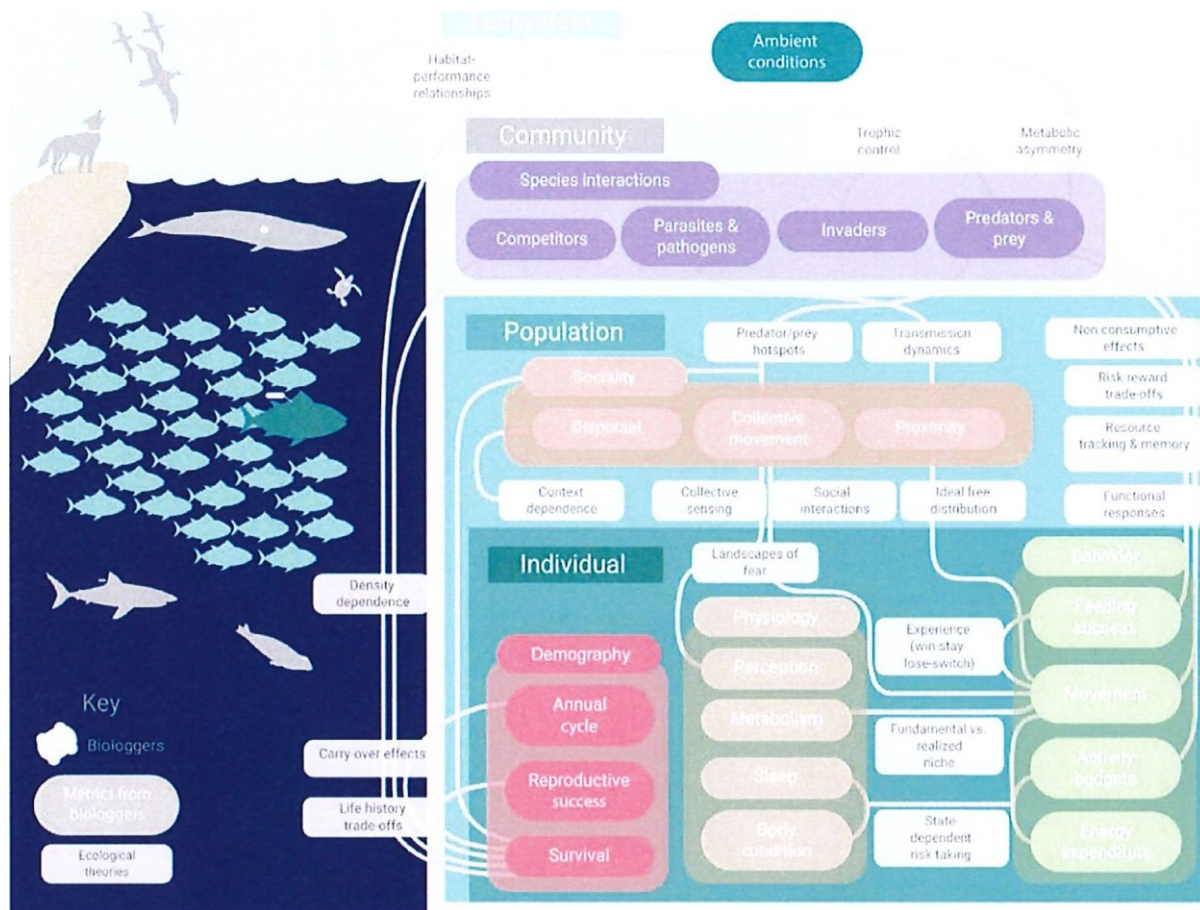
Energy(cost)landscapes: spatial and temporal variation in an animal's cost of moving and foraging, irrespective of energy (gain) landscapes due to resource distribution and abundance. Functional responses: the relationship between an animal's response to a resource and its availability.
Green-wave surfing: migratory animals track and consume high-quality vegetation during green-up in the spring. Resource pulses: sporadic, intense episodes of increased resource availability in space and time. Resource tracking: animals increase energy gain by moving in conjunction with temporal variation in resources across space.
Risk—reward trade-offs: animals balance the need to obtain food rewards while avoiding predation risks. Statedependent risk-taking: body condition mediates how animals navigate riskreward trade-offs.
Vegetation green-up: a burst of vegetation productivity during spring that propagates across landscapes.

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Figure 1. Data generated by archival or transmitting biologgers can be used to calculate extrinsic and intrinsic variables (colored ovals) that can be used to address key research topics (white squares) in behavior and ecology. These research topics span individual, population, community, and ecosystem scales, and cross traditional disciplinary boundaries (red, demography; gold, physiology; green, behavior; orange, sociality; purple, species interactions). Note that there are several critical steps, such as data conversions, processing, and analysis, between raw sensor-derived measurements and the variables presented here (see Table SI in the supplemental information online). For example, species interactions between predators and prey can be measured by pairing accelerometers and acoustic loggers (attached to prey) that measure escape movement responses to predator vocalizations. Illustration by Jessica Kendall-Bar.

Biologging science could be used to address how migratory animals respond to environmental drivers. New technologies are facilitating the measurement of in situ resource distribution and abundance at a sufficiently fine resolution to inform theory about animal movement. For example, Chevallay et al. [46] used a novel animal-borne echosounder to measure prey detection and capture events so that estimates of sensory perception volume could be made. Continuing to ground these research efforts in existing theory (e.g., framing the introduction with previous work on resource patterns such as pulses [47] and waves [48]) can help maximize insights into how movement patterns emerge from stochastic resource patterns such as irregular rainfall or unpredictable fire events. Moreover, testing distinct theories with a common set of data [e.g., predation risk aversion (a top-down

process) and resource tracking (a bottom-up process)] could advance our understanding of how movement outcomes result from risk—reward trade-offs [48].

Biologging for the future

Although many ecological studies that leverage biologging tools have been descriptive, contemporary research can effectively test theory by building on past insights while focusing on generalizable patterns, testing hypotheses, and linking patterns to ecological processes (Figure 2). Many individual examples of biologging studies in both the marine and terrestrial realms test theory (Figure 3). The highlighted studies share many common approaches to their organization and focus, including (i) the introductions are often framed with generalizable patterns in addition to systemspecific information, (ii) the background information often includes theory papers that
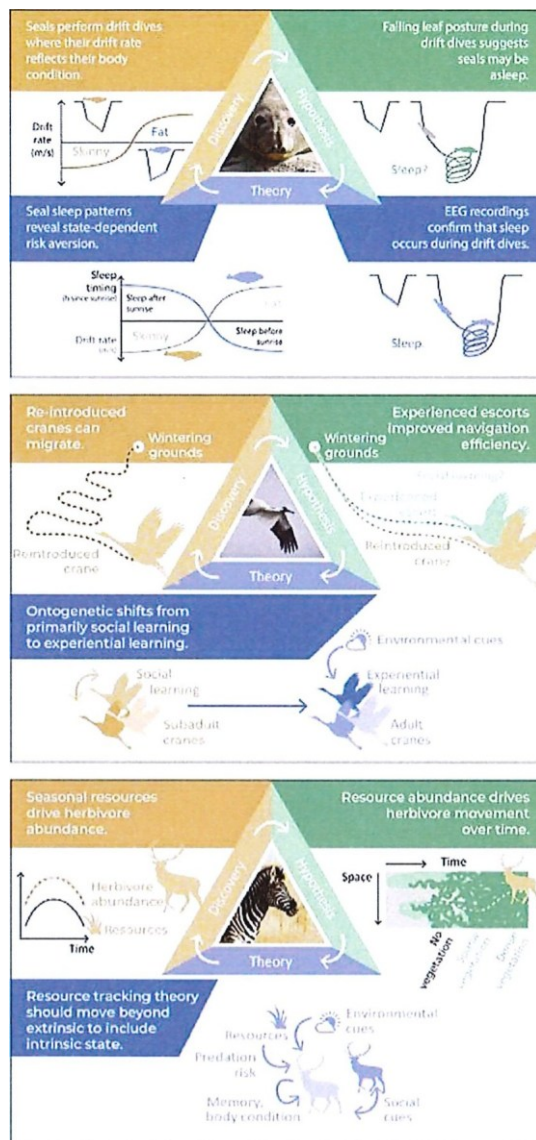
(A) Figure 2. Illustrated examples of the development from discovery to hypothesis and testing to theory refinement for each of three case studies. (A) State-dependent risk-taking throughout migration in northern elephant seals (Mirounga angustirostris). (B) Social and experiential learning in whooping cranes (Grus americana). (C) Migration based on past and current resource availability across species. These case studies show how discoveries and theory testing can comprise a positive feedback loop, where observations lead to insights that inform hypotheses, and testing those hypotheses can lead to theory

(B) development, which can then be refined through continued observations and discoveries.

Illustration by Jessica Kendall-Bar.

Abbreviation: EEG, electroencephalogram.

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in &	Interspecies allometry highlights that female northern elephant seals (Mirounga angustmostns) have high mass-specific diving capacities relative to other diving mammals (87).	Maximum displacement distances for juvenile sea turtles are well beyond those expected for equivalent-sized marine mammals and fishes, but similar to birds (71).	Maximum body size in blue whales (Ba/aenoptera muscu/us) is constrained by prey availability and feeding efficiency (27).

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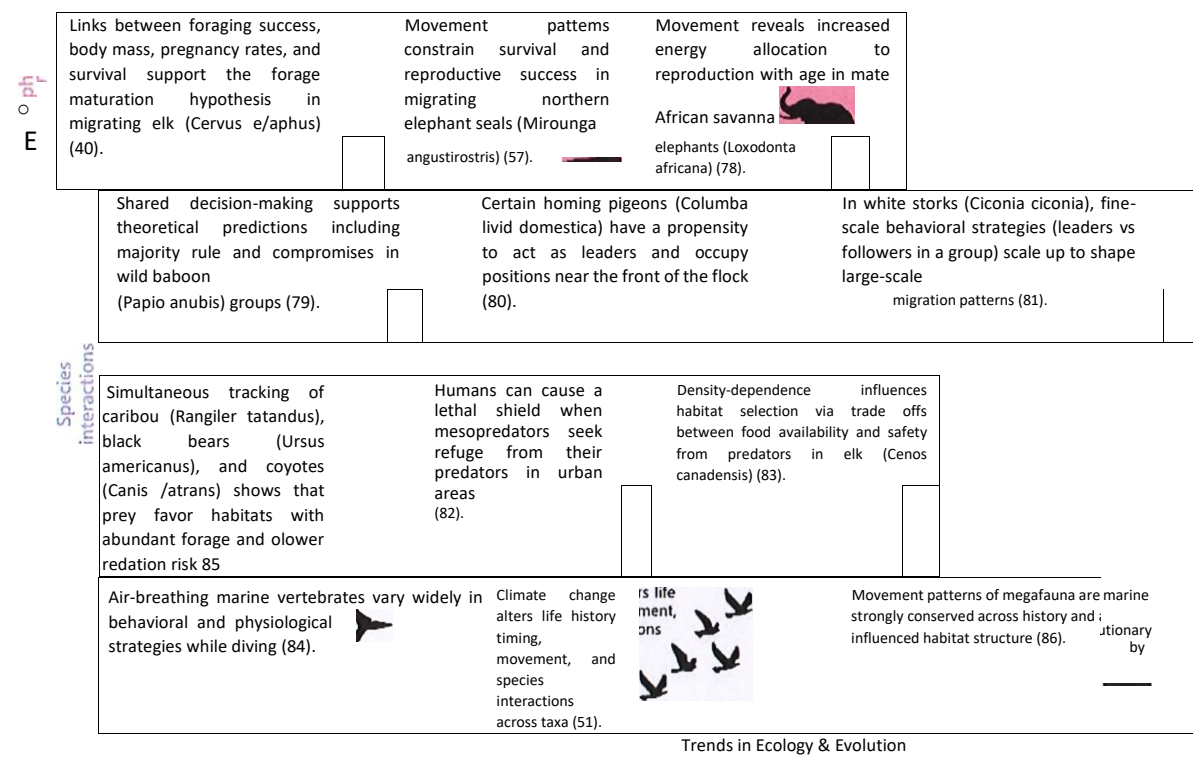| Red muscle endothermy allows some tuna and shark species to achieve faster cruising speeds and more expansive annual migrations (72).	Integration of movement cardiac physiology budgets explain energy driving deficiencies of wild polar bears (Ursus maritimus) due to fragmented sea ice (74).	Metabolic rates and activity behavior with explains mechanisms niche expansion in salmon sharks (lamna dittopis) (73).
Adélie penguins (Pygoscelis ade/iae) exhibit optimal patch residence time in response to dive and bout patch quality (75).	Pumas (Puma conco/o,') increase their kill rates on prey as a response to human-induced fear (76).	Black-browed albatrosses (Tha/assarche melanophris) utilize win-stay, lose-switch strategies to inform foraging decisions using memory and experience (77).

Figure 3. Examples of biologging studies with strong conceptual/theoretical foundations. Studies are organized by discipline and cross levels of biological organization from individuals to populations and ecosystems. See [27,40,51,57,71–87].

The following text appears within the figure:

Links between foraging success, body mass, pregnancy rates, and survival support the forage maturation hypothesis in migrating elk (Cervus e/aphus) (40).

Movement patterns constrain survival and reproductive success in migrating northern elephant seals (Mirounga angustirostris) (57).

Movement reveals increased energy allocation to reproduction with age in mate African savanna elephants (Loxodonta africana) (78).

Shared decision-making supports theoretical predictions including majority rule and compromises in wild baboon (Papio anubis) groups (79).

Certain homing pigeons (Columba livid domestica) have a propensity to act as leaders and occupy positions near the front of the flock (80).

In white storks (Ciconia ciconia), fine-scale behavioral strategies (leaders vs followers in a group) scale up to shape large-scale migration patterns (81).

Simultaneous tracking of caribou (Rangiler tatandus), black bears (Ursus americanus), and coyotes (Canis /atrans) shows that prey favor habitats with abundant forage and olower redation risk 85

Humans can cause a lethal shield when mesopredators seek refuge from their predators in urban areas (82).

Density-dependence influences habitat selection via trade offs between food availability and safety from predators in elk (Cenos canadensis) (83).

Air-breathing marine vertebrates vary widely in behavioral and physiological strategies while diving (84).

Climate change alters life history timing, movement, and species interactions across taxa (51).

Movement patterns of megafauna are marine strongly conserved across history and influenced habitat structure (86).

Species interactions

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inform testable hypotheses, and (iii) the discussions often describe how insights produced from the biologging study advance our theoretical understanding of ecological patterns and processes.

Data synthesis

Many theoretical and conceptual questions require synthesizing multiple biologging datasets. Doing so can produce more generalizable knowledge about patterns and processes in the natural world across vast spatial and temporal scales. Major synthesis efforts include the Tagging of Pacific Predators [49], Retrospective Analysis of Antarctic Tracking Data, [50], Arctic Animal Movement Archive [51], coronavirus disease 2019 (COVID-19) Bio-Logging Initiative [52], and the Wyoming Migration Initiative [53]. Many of these efforts were initially discovery-based but laid a foundation for future concept-driven research. A promising area for future conceptual

research is bridging terrestrial and marine systems. Likewise, re-analyzing and synthesizing datasets can maximize insights and minimize research impacts by reducing the need to instrument additional animals.

Integration of biologging with auxiliary data

Understanding and predicting the spatiotemporal dynamics of populations is a central goal in ecology and conservation, and requires understanding variation in, and genetic and phenotypic drivers of, demographic rates [54-56]. Integrating biologging with auxiliary datasets and complementary disciplines can enable tests of hypotheses that span traditional boundaries (Table Sl). For example, integrating biologging with demographic data from mark—recapture programs could be used to quantify the fitness consequences of movement behavior [57,58l. Moreover, considering species-level traits (e.g., body size, brain size, reproductive characteristics, and diet) when analyzing tracking data [59] or conducting vulnerability risk assessments could facilitate valuable ecological-evolutionary insights. Biologging data can also facilitate insights into human— wildlife conflict theory through field-based experiments that combine camera traps, audio recorders, and biologgers to quantify movement responses to simulated human activity and conservation interventions [60,61].

Novel tools and approaches

Using existing biologging data to address new questions outside those of the initial study is sometimes problematic. In these cases, new tools may be needed to answer a given conceptual question. Here, concept-driven motivation for improved tagging technologies can drive the collaborative development of smaller and longer-lasting biologgers and more reliable sensors that overcome current limitations in measuring the covariates that matter to animals (e.g., in situ resources, predator abundance, multimodal sensory information perception and processing, realtime infection, and heat stress) [62].

Inclusive, equitable practices

More equitable approaches to biologging science, including data collection, processing, archiving, and reporting, will provide the greatest impact and the broadest participation by diverse individuals, institutions, and nations. For example, the research community can seek to understand and preserve the socioecological systems within which the animals exist through global and interdisciplinary collaborators [8], including Indigenous communities who should be compensated for their time and meaningfully involved in study design decisions

based on their knowledge of the system [i.e., development of research question(s), instrumentation size, and handling and attachment methods] [63,64J. Likewise, a global tag registry could help the biologging community

Outstanding questions

How do system-specific findings about ecological patterns and processes generalize across systems?

How can we replicate biologging data collection processes or leverage large datasets across systems or species to test the conditions in which ecological theories are supported?

Which ecological theories are primed for testing or refinement through biologging science?

Which insights from empirical biologging studies are well poised to inform theory development?

How do we engage across disciplinary boundaries to advance, test, and apply ecological theory using biologgers? Who are key partners for removing barriers and fostering interdisciplinary collaborations in this space?

What innovations in biologging technology are needed to facilitate theoretical advancements? How can we accomplish them?
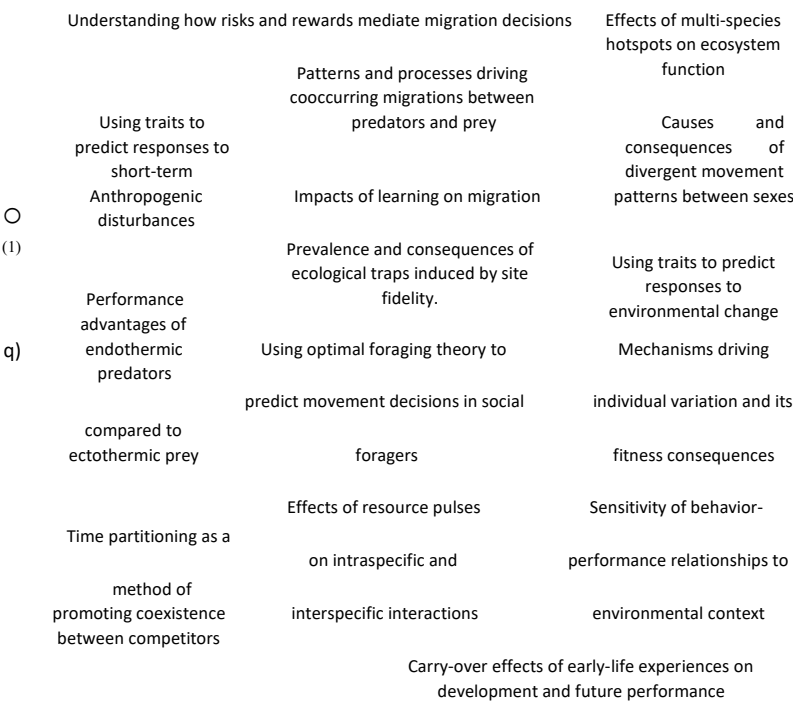
How can we widen the adoption of open science practices among biologging users to accelerate the pace of basic and applied science?

and public know whom to contact about sampling efforts and datasets to optimize the probability and efficiency of collaboration [65]. Standardized and reproducible data can fast-track theorytesting across systems by facilitating

synthesis of large global biologging datasets [66J. This is especially needed for nonspatial data such as physiologging, accelerometry, and video data that do not fit the standards developed for spatial data [67]. Open-access publication of those datasets must credit those who collect and share data [68]. Finally, partnering with theoreticians will allow empiricists to identify promising areas for theory development and refinement using biologging data.

Concluding remarks

There is a wide range of novel research directions that can be pursued with biologgers, ranging across temporal and spatial scales (Figure 4,• see Outstanding questions). The key to moving from anecdote to generalizable theory is to examine interdisciplinary patterns and processes across species and habitats. For example, habitat selection can be influenced by the population context (e.g., density and social dynamics), by the community context (e.g., predators and

Contextual differences between physiological theory and empirical behavioral data Incorpora

bioenergetic life history theory

Relationships between theoretical tolerance landscapes (e.g. Effects of climate change temperature), anatomy, and performance in wild animals on site selection

Understanding how risks and rewards mediate migration decisions

Effects of multi-species hotspots on ecosystem function

Patterns and processes driving cooccurring migrations between predators and prey

Using traits to predict responses to short-term Anthropogenic disturbances

Causes and consequences of divergent movement patterns between sexes

Impacts of learning on migration

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Prevalence and consequences of ecological traps induced by site fidelity.

Using traits to predict responses to environmental change

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Performance advantages of endothermic predators compared to ectothermic prey

Using optimal foraging theory to predict movement decisions in social foragers

Mechanisms driving individual variation and its fitness consequences

Time partitioning as a method of promoting coexistence between competitors

Effects of resource pulses on intraspecific and interspecific interactions

Sensitivity of behavior-performance relationships to environmental context

Carry-over effects of early-life experiences on development and future performance

Days
Weeks
Months
YearsDecades

Temporal scales

rends in Ecology & Evolution Figure 4. Some emerging research directions that could be addressed using biologgers, across temporal and spatial scales. Each topic is colored by discipline (blue, morphology; gold, physiology; green, behavior; red, demography; orange, sociality; purple, species interactions; gray, cross taxa). Many of the featured research topics are moderately well understood from a theoretical perspective but are primed for empirical testing through finer-resolution or larger-scale

biologging data. For others, extensive empirical data could challenge or refine theory by identifying deviations from optimality or highlighting discrepancies between theory and empirical data. Many topics represent significant opportunities for developing both theory and empirical evidence, especially across disciplinary boundaries. All can be used as an agenda for further research and a benchmark for future evaluations of progress in biologging science.

competitor density), and by the environmental context (e.g., drought, fire) (Figure 1). Similarly, theory can be applied to the many roles played by humans (e.g., predators, resource drivers, disease sources) to inform conservation and management actions such as reserve design and species protection [69]. Predictive models used for these decisions will be most accurate when informed by a process-based understanding of animal movements and their roles in ecological systems [70]. For example, understanding how animals move relative to human-made barriers such as fences and highways can allow predictions about how

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increasing urbanization and development will reduce wildlife fitness as the human population grows. Likewise, characterizing links between animal performance and environmental conditions can facilitate predictions of how climate change will trigger species range shifts and population declines.

Biologging enables efficient, fine-scale data collection that can provide the breadth and depth needed to develop, test, and refine our understanding of ecological processes in our rapidly changing world (Figure 2). Although new theories are rare in ecology, new technological developments can allow existing theories or hypotheses to finally be tested or refined, so long as the research has a strong conceptual focus (Figure 3) [58]. Of course, theory testing and refinement are not always possible. Research is still in the description and discovery phase for species that have never been instrumented or that inhabit under-studied regions and biomes. In these cases, a closer connection between conceptual questions and biologging technology can expedite the development of new theories and contribute to the iterative process of testing and refinement [7]. Through these avenues, biologging can provide insight into how nature works and provide a roadmap for better protection of species, ecosystems, and the services they provide [681.

Declaration of interests

The authors declare no competing interests.

Supplementary information

Supplementary information associated with this article can be found online at https://d0i.org/10.1016/j.tree.2024.09.009.

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