# Biologging for the future: how biologgers can help solve fundamental questions, from individuals to ecosystems

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## 1. Abstract

Archival instruments attached to animals (biologgers) have enabled exciting discoveries and have promoted effective conservation and management for decades. Recent research indicates that the field of biologging is poised to shift from pattern description to process explanation. Here we describe how biologgers have been - and can be - used to test hypotheses and challenge theory in behavior and ecology through three case studies and many short examples. These examples, spanning predator-prey interactions, state-dependent risk-taking, resource tracking, and collective movement decisions, show how biologging can resolve long-standing mysteries if research is designed with a solid conceptual foundation. The next phase of biologging science will require scaling studies from individuals to populations and possibly to ecosystems. It will also benefit from building equitable international and interdisciplinary partnerships, bridging the terrestrial-marine divide, and addressing ethical conundrums including animal handling and open science practices. Doing so will help cement biologging as an indispensable tool for producing generalizable knowledge about how organisms and ecosystems function.

## 2. Background

A holistic understanding of complex ecological processes requires creative solutions for measuring broad-scale, high-resolution data across sites, species, and systems. Archival instruments attached to animals (hereafter, "**biologgers**") have become routine tools for recording physiological, behavioral, and demographic characteristics of individuals, and their interactions with environmental and ecological features [1] (Figure 1).

The inception of biologging enabled novel discoveries such as understanding how animals migrate across the globe relative to their prey and predators, including questions at temporal and spatial scales that far exceed those from traditional approaches. Like other technologically-driven disciplines including astronomy and genetics, biologging is poised to shift from pattern discovery to designing studies with strong conceptual underpinnings [2]. Biologging studies have transitioned from providing unique observations to adopting a rigorous scientific approach in recent years. Researchers now formulate defined questions, ensure adequate sample sizes, and conduct in-depth analyses, shifting from simple movement descriptions to hypothesis-driven investigations. For example, biologgers have provided data on foraging success, which can be used to test hypotheses about functional response types, risk-reward trade-offs, and resource tracking (Figure 1).

Biologging studies have also applied "big-data" approaches to tackle behavioral and ecological mechanisms underlying movements and the proximate internal and external factors that constrain them (Figure 1) [3]. In turn, the discoveries and natural history descriptions enabled by new technology are primed for the testing and refinement of long-standing theories [4], with implications for broad generalizations [5] and evidence-based conservation solutions [6]. The next step is to answer questions that span multiple taxa, such as whether generalizable "rules" underpin complex movements and species interactions [7].

For many of these outstanding questions, ecological theory exists to generate hypotheses about how animals behave and how behavior scales to ecosystem processes such as distribution and abundance across trophic levels [8]. Previous empirical tests of many theories have been limited to controlled laboratory experiments. In contrast, biologging in natural settings enables precise measurements in ecologically relevant contexts where competing selective pressures such as predation, starvation, and infection exist. Thus, biologging is perfectly positioned to test many hypotheses from long-standing ecological theories that are underpinned by animal behavior.

## 3. Objectives

The rapid development of biologging has motivated numerous proposals for future directions. Previous researchers have urged the biologging community to integrate with other disciplines [9], use mathematics and optimality [9,10], re-unite big data approaches with field-based ecological processes [11], target key knowledge gaps [12], and reconnect tools and questions [13,14]. We believe a key next step is to test long-standing ecological theories through biologging studies, and to identify areas of intensive data collection that are well-positioned to bridge this gap. *This review aims to illustrate how biologging is uniquely suited to test hypotheses and refine theory because it can integrate complexity into mechanistic tests.* First, we describe three case studies (representing state-dependent behavior, learning, and memory) and many example publications in which observational data led to discoveries that were then leveraged to test hypotheses and develop robust conceptual frameworks. Second, we identify outstanding questions in ecological theory that would be best addressed with large-scale integration of biologging studies across systems. Finally, we discuss practical steps toward theory-grounded biologging through data synthesis across the terrestrial-marine divide, concept-driven motivation for technology development, open data practices, and intentional interdisciplinary partnerships.

## 4. Examples of development from discovery to theory

We provide three case-studies below that range from single-species behavioral research to multispecies interactions and consequences for population dynamics (Figure 2). 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 development, which can then be refined through continued observations and discoveries. In addition to summarizing key findings, we propose directions for future research questions that could be addressed with targeted biologging studies or comparative studies using existing data grounded in conceptually solid foundations.

### 4.1. State-dependent risk-taking throughout migration in elephant seals

Body condition has been hypothesized to mediate how animals navigate risk-reward trade-offs; however, the difficulty of measuring body condition, predation risk, and food rewards in the wild has limited our understanding of how intrinsic states affect risk-taking behavior [15]. Biologgers have begun to address this gap by collecting data on animal movement behavior; pioneering time-depth recorders facilitated the discovery that elephant seals cease swimming and passively drift during some dives [16]. These so-called "drift dives" often occur after foraging bouts, and seals with less body fat at the start of the foraging trip sink faster [17]. Later, drift rates were validated against longitudinal energy gain rates [18] as a valuable metric for estimating body composition [19] at fine spatio-temporal scales throughout migrations. At the same time, inertial measurements of drifting seals provided further support for hypotheses about the functions of drift dives for resting and food processing [20]. Finally, biologgers were used to confirm that seals sleep during drift dives [21] and derive body composition estimates and ethograms at a daily scale throughout months-long migrations to test predictions from state-dependent risk aversion theory about when animals should rest and forage [22]. This three-decade research arc examining whether behavior is state-dependent throughout oceanic migrations suggests that seals in superior body condition sacrifice more profitable nocturnal foraging hours to sleep in the safety of darkness (Figure 2) [22].

When grounded in a strong conceptual framework, the development of new technologies and analytical approaches holds great promise for studying 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 species that do not perform drift dives [23]. Likewise, other components of an animal's internal state (e.g., hunger, heat, stress, exhaustion [24]) may influence behavior and could be measured with new sensors. Could new physiological biologgers that measure brain activity [25] and heart rate [26] be used to test theories of physiological recharge, rebound, and replenishment (e.g., sleep quotas) in other species [27]? Can we simultaneously instrument predators and prey to parse spatial and temporal dimensions of risk and reward in "dynamic landscapes of fear" or "dynamic energy landscapes" theoretical frameworks [28,29]?

### 4.2. Social and experiential learning in whooping cranes

How animals learn long-distance migrations is an outstanding question that has implications for wildlife conservation and management including the designation of protected areas and strategic planning of species re-introductions. The role of social versus experiential learning in migratory behavior has been tested in studies of re-introduced whooping cranes (*Grus americana*) (Figure 2). Using satellite transmitters and VHF tags, movements and survival of re-introduced whooping cranes demonstrated successful migration and dispersal patterns [30]. A decade later, a reanalysis of these data tested the hypothesis that re-introduced cranes migrate more efficiently when flying with experienced birds [31]. More recently, researchers used a long-term satellite tracking dataset to discover an ontogenetic switch from social to experiential learning as birds age, allowing them to track resources throughout their migration at all ages [32]. This work transitioned from initial descriptive discoveries (examining whether re-introduction was a successful management strategy) to theory-testing (disentangling the roles of social versus experiential learning) and laid the groundwork for testing many long-standing ecological questions. For example, if social learning is a primary mechanism by which movement strategies evolve, will interrupted information transfer have population-level consequences [33]? How do implicit or explicit social cues influence the timing of animal migrations [34]? How do migratory animals gain information from other species [35]? To what extent does social learning shape the outcomes of predator–prey interactions and demographic processes [36]?

### 4.3. Migration based on past and current resource availability across species

Strong 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 [37]. 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 1970's, researchers observed simultaneous changes in plant phenology and migratory movements in waterfowl [38]. Later, biologgers were used to examine the link between **vegetation green-up** and ungulate migration decisions [39]. Follow-up studies tested hypotheses that mule deer migrate in concert with green-up, maximizing energy intake rather than speed [40], and that the rate and order of green-up influences the ability of animals to **green-wave surf** [41]. Simulation of zebras and mule deer and empirical validation with GPS tracks showed that previous experience (memory) with green-up patterns also plays an essential role in migration [42,43]. More recently, data analysis from biologgers suggested revising the theory about the relative roles of memory [44] and proximate cues [34] in the movement of terrestrial and marine animals.

Biologging can help us address the interplay of animal migrations in response to environmental drivers. Questions that can be addressed include: What movement patterns emerge in response to stochastic resource patterns (i.e., neither pulses nor waves) [45,46]? How can *in situ* resource availability be measured (instead of inferred from physical environmental metrics) at a sufficiently fine resolution to inform theory about animal movement, especially in 3-dimensional ocean environments [47,48]? Can we unite theory examining predation risk and resource tracking to integrate top-down and bottom-up processes in estimating risk-reward trade-offs and optimal decision-making during migration [49]? In turn, can we develop and revise theories about how animals contribute to resource pulses and environmental predictability through environmental feedback [50]? For example, one could determine if migratory marine megafauna that serve as ecosystem engineers promote a green wave of productivity that sustains themselves and their ecosystems, like bison in terrestrial systems [51]. Biologging data are uniquely suited to understand how animals respond to and influence resource pulses, particularly in a changing world.

### 4.4. Examples in other sub-disciplines.

There are many additional examples of biologging studies in both the marine and terrestrial realms that successfully test theory and/or have strong conceptual foundations. In Figure 3, we provide short summaries of studies spanning a broad set of sub-disciplines including Morphology, Physiology, Behavior, Demography, Sociality, Ecology and Cross-taxa studies and crossing levels of biological organization from individuals to populations and to ecosystems (Figure 1). These examples demonstrate how biologging scientists can maximize the impact of their work by ensuring that theoretical concepts ground our research (e.g., Figure 3), regardless of whether the work is more motivated by pattern (inductive) or by theory (deductive) [52].

## 5. Outstanding Questions

Emerging questions that can be answered with biologgers, ranging across temporal and spatial scales, are provided in Figure 4. Many of the highlighted questions are moderately well understood from a theoretical perspective but are primed for empirical testing through finer-resolution or larger-scale biologging data. For other questions cases, extensive empirical data could challenge or refine theory by identifying deviations from optimality or highlighting discrepancies between theory and empirical data. Many cases 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.

## 6. Roadmap for the Future

### 6.1. Big data syntheses

Synthesis of multiple biologging datasets with extensive breadth and depth can produce generalizable knowledge about patterns and processes in the natural world across vast spatial and temporal scales (Figure 4). Recent efforts include the Tagging Of Pacific Predators [53], Retroactive Analysis of Antarctic Tracking Data, [54], Arctic Animal Movement Archive [55], COVID-19 Bio-Logging Initiative [56], and Wyoming Migration Initiative [57]. Many of these efforts were necessarily discovery-based but laid a foundation for future concept-driven research, such as answering questions like: Can we identify multispecies hotspots in three-dimensional space and time? What role do these hotspots play in ecosystem function (Figure 4)? Re-analyzing and synthesizing datasets can maximize insights and minimize research impacts including animal handling. A promising area for future conceptual research is bridging terrestrial and marine systems. For example, terrestrial studies often include *in situ* focal follows to interpret biologging data [58]. In contrast, marine studies commonly bridge the spatio-temporal scales between coarser environmental and finer movement parameters by integrating environmental sensors into biologgers [14,59]. The few studies that span the marine-terrestrial interface have produced valuable comparative insights [60] and deepened our understanding of relationships between land and sea [61].

### 6.2. Interdisciplinary integration

Integrating biologging with complementary disciplines can also generate new theory and hypotheses at the interfaces between the two [62]. For example, including genomic and demographic covariates could help disentangle the contributions of genetic mechanisms, ontogeny, and senescence to animal movement patterns [63,64]. Similarly, combining mark-recapture studies with biologging studies could help elucidate the fitness consequences of movement [65,66]. Merging trait databases (e.g., inter-specific variation in body size, brain size, sensory organs, reproductive characteristics, and diet [67]) with tracking data [68] or vulnerability risk assessments [69] could facilitate large-scale ecological-evolutionary insights (Figure 4). Alternatively, using biologgers to measure traits and putting those traits into an eco-evo framework can provide insightful phylogenetic contexts for behaviors and species interactions [70–72].

Biologging data can also facilitate field-based experimental biology by allowing for the quantification of movement responses to experimental treatments such as simulated human activity [73]. Long-duration interdisciplinary studies that span a range of environmental conditions and extreme events are necessary to predict future changes and answer a key outstanding question: How sensitive are behavior-performance relationships to environmental context (Figure 4) [62,74]? Understanding and predicting the spatio-temporal dynamics of populations is a central goal in ecology and conservation, and requires understanding variation in, and genetic and phenotypic drivers of, demographic rates [75–77].

Another emerging interdisciplinary direction is field sensory biology, which focuses on the detection of prey by predators [47] and less commonly the detection of predators by prey [78]. Future biologging studies of feeding behavior and prey detection can help address questions including, including how animals perceive and respond to multimodal sensory information (vision, olfaction, tactile, acoustic) in natural systems [79]? How can biologgers measure how animals produce and perceive auditory cues to respond to conspecifics, heterospecifics, and their environment [80]? How is sensory perception built into an animal's cognitive map of its environment [81,82]?

### 6.3. Novel tools, approaches, and theories

Using existing biologging data to address new questions outside those of the initial study is sometimes problematic. New tools, approaches, or theories may be needed to answer a given conceptual question in these cases**.** Here, concept-driven motivation for improved tagging technologies can drive the collaborative development of smaller biologgers and more reliable sensors that overcome current limitations in measuring the covariates that matter to animals (e.g., *in situ* resources, predator abundance, real-time measurements of endocrine markers, infection status, or heat stress). For example, the recent use of real-time monitoring [83], back-mounted accelerometers [84], and underwater cameras triggered by accelerometry during feeding attempts [85] have facilitated conceptual advances in movement decisions, interspecific communication, and resource acquisition. In some cases, this may require the integration of several theories; for example, can we unite the Landscape of Fear with the Landscape of Disgust theories to empirically test how animals navigate the risks of mobile parasites and predators [86–88]?

### 6.4. Inclusive, equitable biologging

More collaborative and diverse teams facilitate innovation and transformative scientific insights [89,90]. 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 socio-ecological systems within which the animals operate through global and interdisciplinary collaborators [14], including Indigenous communities who can be compensated for their time and meaningfully involved in instrumentation decisions. Likewise, a global tag registry could help the biologging community know who to contact about sampling efforts and datasets [91]. Standardized and reproducible data can fast-track comparative biological analyses and interdisciplinary research using biologgers [92] by ensuring that data are both available and usable. This is especially needed for non-spatial data such as physiologging, accelerometry, and video data that do not fit the standards developed for spatial data [93]. Open-access publication of those datasets could credit those who collect and share data [68].

## 7. Concluding Remarks

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 competitor density), and by the environmental context (e.g., drought, fire) (Figure 1). 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. Research with a conceptual focus is often more impactful and can provide insights across various disciplines and systems (Figure 3) [66]. Moreover, predictive models used in management and conservation will be most accurate when they are informed by process-based understandings of animal movements and their roles in ecological processes [94].

Similarly, theory can be applied to humans in their roles as shields (creating a spatial refuge 'shielding' prey from predators) [95], predators, resource drivers, disease sources, and tested with biologgers to inform conservation and management actions [96]. 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. 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 [13]. We believe biologging can have "unimaginably important applications" [62] and address new ideas by focusing on theory-driven hypothesis testing. Through these avenues, biologging can illuminate how nature works and thus provide a roadmap for better protection of species, ecosystems, and the services they provide [68].

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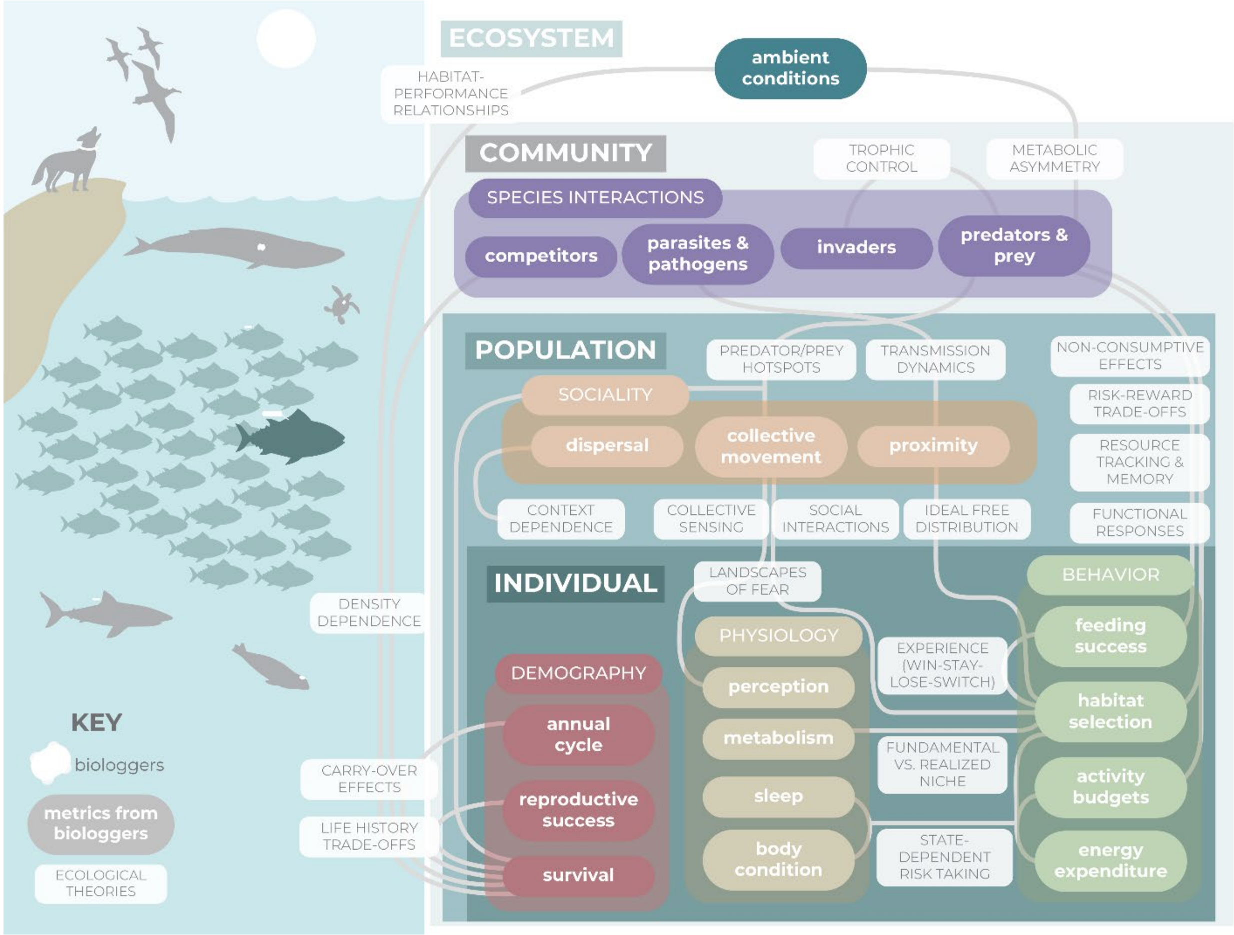


**Figure 1.** Archival or transmitting biologgers measure extrinsic and intrinsic variables (colored circles) that can be used to address key research topics (white squares) in behavior and ecology across scales from individuals to populations to communities and ecosytems.

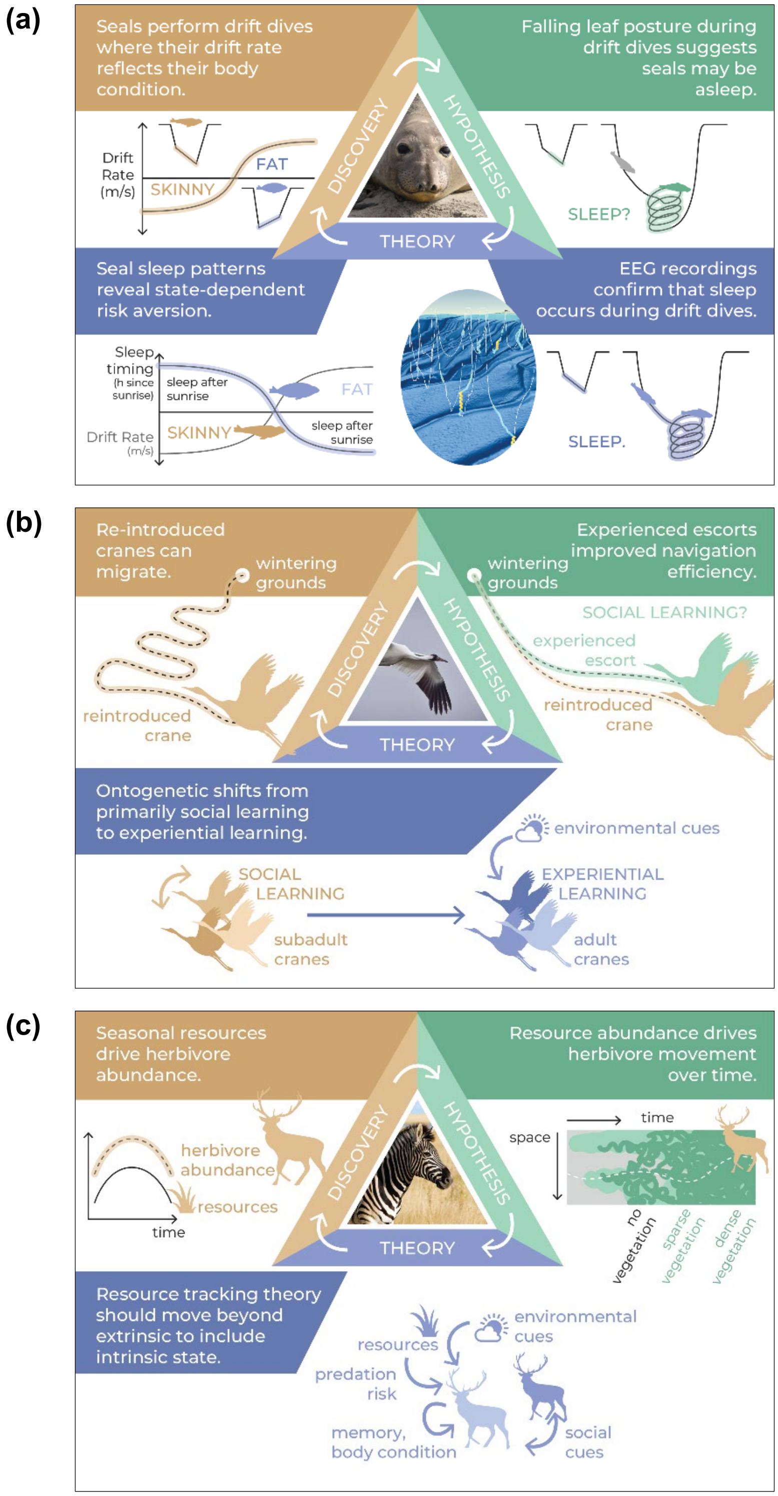
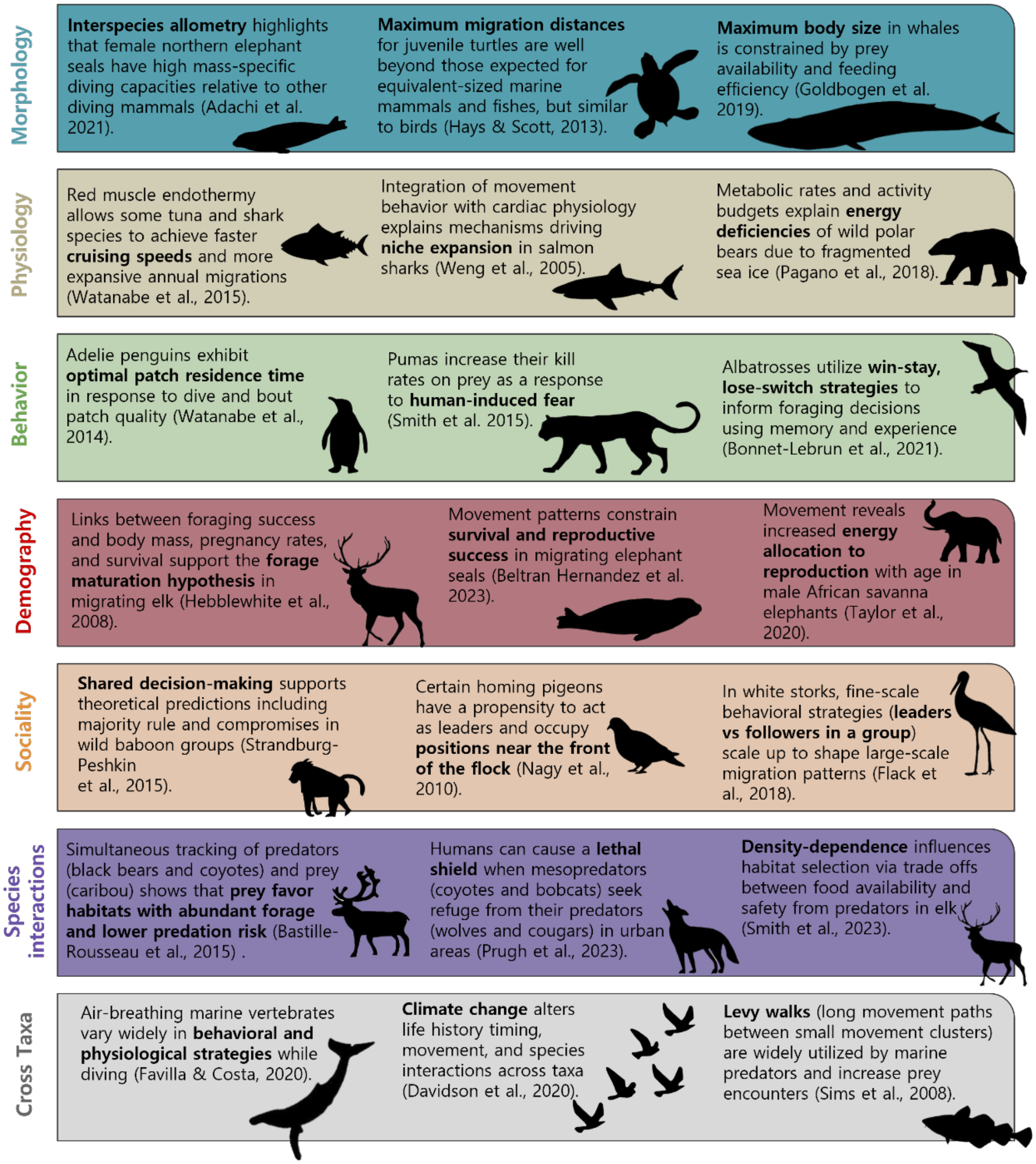


**Figure 2.** Illustrated examples of the development from discovery to hypothesis testing to theory refinement for each of three case studies: **(a)** state-dependent risk taking throughout migration in elephant seals, **(b)** social and experiential learning in whooping cranes, and **(c)** migration based on past and current resource availability across species.



**Interspecies allometry** highlights that female northern elephant seals have high mass-specific diving capacities relative to other diving mammals (Adachi et al. 2021).

**Maximum migration distances** for juvenile turtles are well beyond those expected for equivalent-sized marine mammals and fishes, but similar to birds (Hays & Scott, 2013).

**Maximum body size** in whales is constrained by prey availability and feeding efficiency (Goldbogen et al. 2019).

Red muscle endothermy allows some tuna and shark species to achieve faster **cruising speeds** and more expansive annual migrations (Watanabe et al., 2015).

Integration of movement behavior with cardiac physiology explains mechanisms driving **niche expansion** in salmon sharks (Weng et al., 2005).

Metabolic rates and activity budgets explain **energy deficiencies** of wild polar bears due to fragmented sea ice (Pagano et al., 2018).

Adelie penguins exhibit **optimal patch residence time** in response to dive and bout patch quality (Watanabe et al., 2014).

Pumas increase their kill rates on prey as a response to **human-induced fear** (Smith et al. 2015).

Albatrosses utilize **win-stay, lose-switch strategies** to inform foraging decisions using memory and experience (Bonnet-Lebrun et al., 2021).

Links between foraging success and body mass, pregnancy rates, and survival support the **forage maturation hypothesis** in migrating elk (Hebblewhite et al., 2008).

Movement patterns constrain **survival and reproductive success** in migrating elephant seals (Beltran Hernandez et al. 2023).

Movement reveals increased **energy allocation to reproduction** with age in male African savanna elephants (Taylor et al., 2020).

**Shared decision-making** supports theoretical predictions including majority rule and compromises in wild baboon groups (Strandburg-Peshkin et al., 2015).

Certain homing pigeons have a propensity to act as leaders and occupy **positions near the front of the flock** (Nagy et al., 2010).

In white storks, fine-scale behavioral strategies (**leaders vs followers in a group**) scale up to shape large-scale migration patterns (Flack et al., 2018).

Simultaneous tracking of predators (black bears and coyotes) and prey (caribou) shows that **prey favor habitats with abundant forage and lower predation risk** (Bastille-Rousseau et al., 2015) .

Humans can cause a **lethal shield** when mesopredators (coyotes and bobcats) seek refuge from their predators (wolves and cougars) in urban areas (Prugh et al., 2023).

**Density-dependence** influences habitat selection via trade offs between food availability and safety from predators in elk (Smith et al., 2023).

Air-breathing marine vertebrates vary widely in **behavioral and physiological strategies** while diving (Favilla & Costa, 2020).

**Climate change** alters life history timing, movement, and species interactions across taxa (Davidson et al., 2020).

**Levy walks** (long movement paths between small movement clusters) are widely utilized by marine predators and increase prey encounters (Sims et al., 2008).

**Figure 3.** Examples of biologging studies with strong conceptual/theoretical foundations. Examples are organized by discipline. See references for full citations [39,55,58,65,70,72,95,98–111].

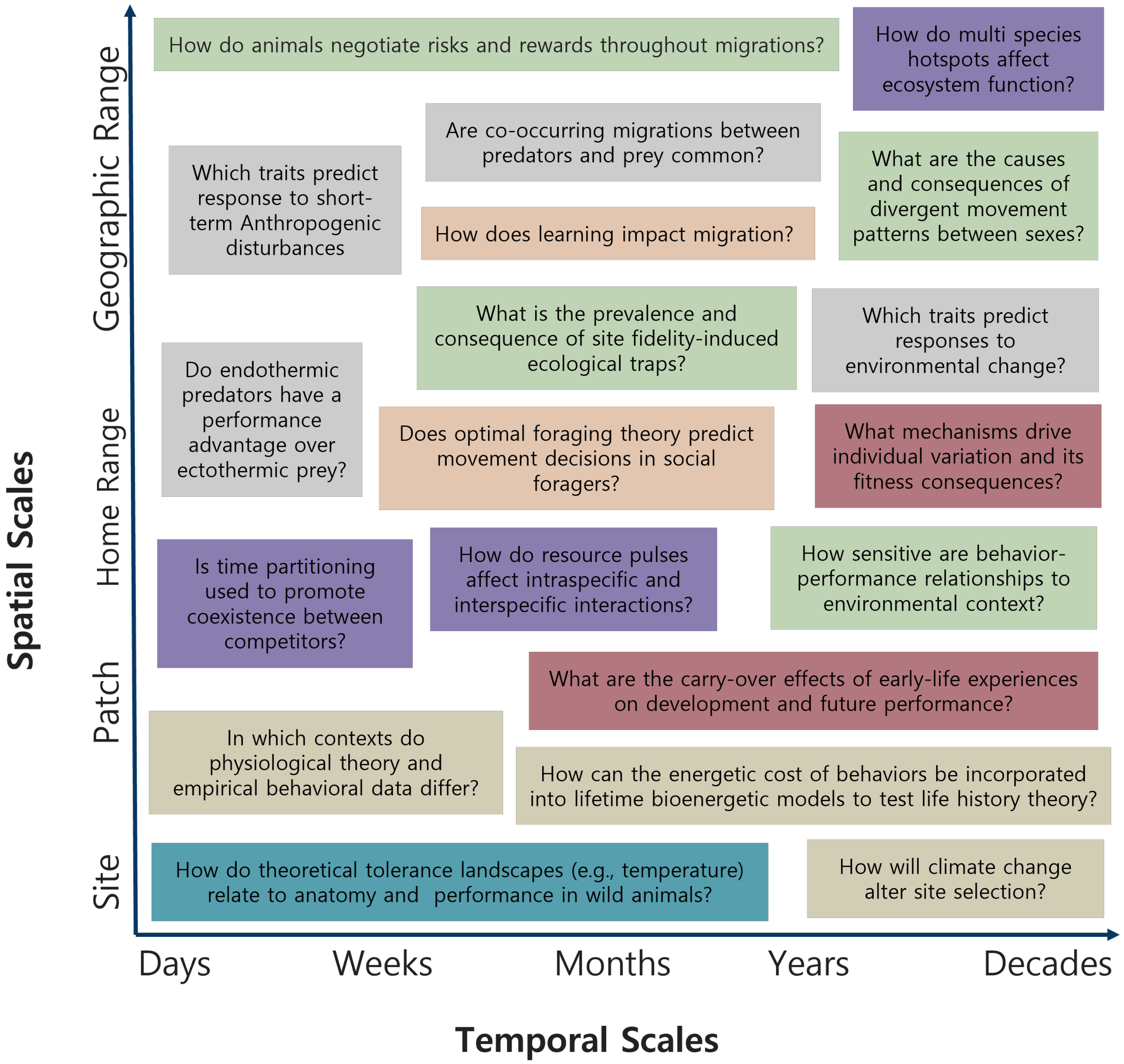


**Figure 4.** Some promising areas of research that could be addressed using biologgers, across temporal and spatial scales. Colored by discipline (see Fig 4 for key).