Trends in
Ecology & Evolution

Forum

Extensive behavioral data contained within existing ecological datasets

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Long-term ecological datasets contain vast behavioral data, enabling the quantification of among-individual behavioral variation at unprecedented spatiotemporal scales. We detail how behaviors can be extracted and describe how such data can be used to test new hypotheses, inform population and community ecology, and address pressing conservation needs.

Importance of individual behavioral variation in a changing world

Consistent intraspecific behavioral variation, sometimes referred to as 'personality', has consequences for every level of ecological organization (Figure 1), affecting individual survival, population dynamics, and community-level interactions such as seed dispersal [1], disease transmission, and the structure and functioning of ecosystems (reviewed by [2]). Understanding the forces that structure and maintain among-individual behavioral variation is also important because behavior is an essential aspect of how organisms, species, and communities will respond to global change. Indeed, a change in behavior can be the earliest warning sign of extinction or foreshadow trophic collapse [3] and provides a means to predict shifts in critical interactions within novel ecosystems [4,5]. Although consistent behavioral variation has individual-level consequences that are well studied [2], our understanding of its implications for populations, communities, and ecosystems is limited by the challenge of repeatedly measuring labile behavior in many individuals across large geographic areas. Studies that use animal-borne sensors for location-based tracking and biologging in terrestrial (e.g., ungulates, wolves) and marine (e.g., fish, cetaceans, sea turtles) environments [6] illustrate the value of collecting individual behavioral data over large spatial and temporal scales. However, the logistical and financial challenges of such studies can limit their geographic scope and duration [7].

The large, distributed, long-term data collection networks that characterize the age of 'big data' [8] provide an unprecedented opportunity to quantify large-scale, long-term variation in animal behavior. This opportunity arises because these networks, although typically focused on populations and communities, gather abundant repeated behavioral measurements from individuals across wide geographic areas.

Big behavioral data (BBD) from existing datasets

Several long-term distributed data collection networks exist that monitor vertebrates using consistent methods. In North America, examples include the Long Term Ecological Research Network[i], the National Ecological Observatory Network[ii] (NEON), the Institute for Bird Populations' Monitoring Avian Productivity and Survivorship program[iii] (MAPS), and the Pacific States Marine Fisheries Commission's Columbia Basin PIT Tag Information System[iv] (PTAGIS). Beyond North America, examples include Movebank[v], a global online database of animal tracking data, and the European Tracking Network[vi], a pan-European biotelemetry network (ETN). Here, we focus on three North American data-collection networks (Figure 1) for their wealth of data and user-friendly data access, query builders, and **exploration** (see Glossary) tools. For a nonexhaustive list of additional global projects and open data repositories

Glossary

Activity: the general level of activity or locomotor behavior of an individual.

Boldness: an individual's propensity to take risks or respond in a risky situation. Individuals exist along a spectrum from timidness (or fearfulness) to boldness.

Exploration: the tendency of an individual to seek out and/or investigate novel or unfamiliar environments, food, or objects.

Behavioral axes: the primary dimensions along which behavior can vary and that characterize the diversity and complexity of behaviors observed in individuals or populations. The major axes that have been proposed to describe behaviors observed in animals include boldness, activity, exploration, aggression, and sociability.

Mean-standardized individual variation: the proportion of phenotypic variation in a trait relative to the trait mean that can be attributed to among-individual differences in trait expression. Using a mean-standardized measure of variation is preferred to variance standardized measures (such as repeatability) when comparing variance between populations, sexes, etc., because ratios of among-individual and total variance in two populations can be equal despite differences in both numerator and denominator.

Pace-of-life syndrome (POLS) hypothesis: a hypothesis suggesting that among-individual variation in behavior may be maintained because suites of phenotypic characteristics (e.g., behavioral, morphological, physiological, life history) covary to balance trade-offs between current and future reproduction and allow individuals with different strategies to achieve similar fitness.

Resource selection: the use of a resource that is disproportionate to the availability of the resource.

Sociability: an individual's tendency to seek the presence of conspecifics.

Spatial niche specialization: intraspecific variation in spatial dimensions of the ecological niche.

State-dependent feedbacks: a major ecological hypothesis explaining the maintenance of consistent individual behavioral variation. This hypothesis refers to reciprocal interactions between state (intrinsic or extrinsic) and behavior, whereby individuals differ in behavior as an adaptive response to state differences, and resulting behavioral differences influence subsequent differences in state.

Trap diversity: the tendency of an individual to use new versus previously used trap locations upon subsequent captures. Trap diversity is commonly used to infer the willingness to explore novel environments (exploration).

Trappability: the tendency of an individual to be captured (or recaptured). Trappability is commonly used to infer the willingness to take risks (boldness).

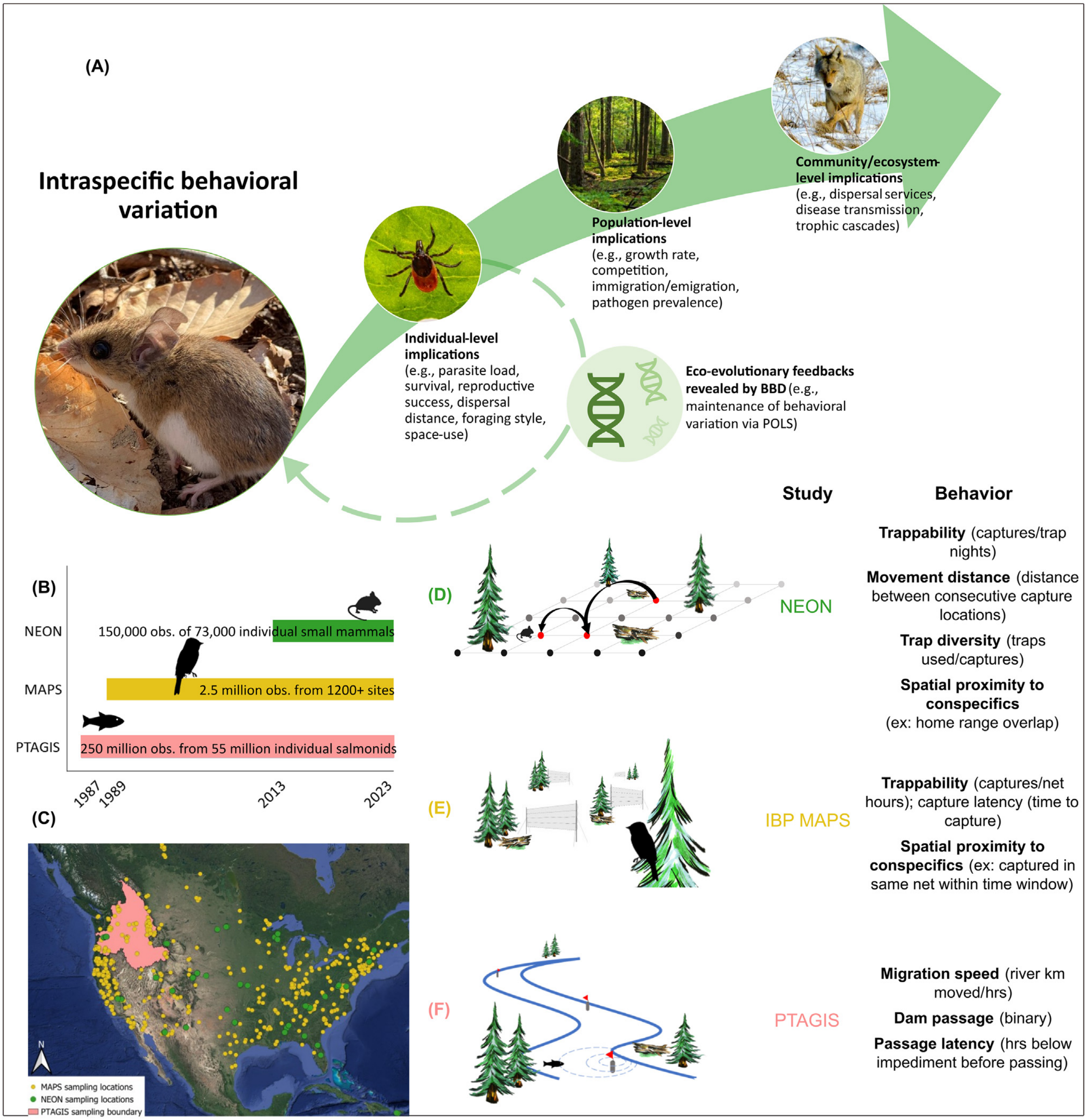

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Figure 1. Existing ecological datasets contain extensive information about the behavior of individual animals at broad temporal and geographic scales. (A) Big behavioral data (BBD) quantified from existing North American ecological datasets reveal implications at multiple scales and uncover ecoevolutionary feedbacks such as the maintenance of among-individual behavioral variation via pace-of-life syndromes (POLS). (B,C) Distributed ecological networks enable quantification of animal behavioral variation across unprecedented spatiotemporal scales in terrestrial and freshwater systems. Examples include (D–F) the National Ecological Observatory Network (NEON) small mammal box trapping, the Institute for Bird Populations' Monitoring Avian Productivity and Survivorship program (MAPS), and the Pacific States Marine Fisheries Commission's Columbia Basin PIT Tag Information System (PTAGIS), respectively. (D) Behaviors derived from individual capture histories, the location of each observation, and the spatiotemporal proximity to conspecifics can provide insight into individual variation in boldness,

(Figure legend continued at the bottom of the next page.)

where BBD can be found, see [9] and the supplemental information online.

A key component of NEON's small mammal sampling, MAPS's bird monitoring, PTAGIS's fish migration and survival data, and data from other projects and repositories (see the supplemental information online) is that individuals are uniquely marked, and each encounter is paired with information about the location and time of the observation. Such datasets, therefore, comprise repeated information about individual movements and space use (Figure 1). For example, from repeated encounters of birds and small mammals, we can quantify individual **trappability** and **trap diversity**, which may be interpreted as measures of **boldness** and exploration, respectively [10]. From repeated movements of tagged fish, we can quantify each individual's migration speed (Figure 1), which can be used to assess individual variation in locomotor **activity**, or the latency to pass impediments in the watershed, which may be used to infer boldness. For guidance on accessing data and example queried datasets from NEON, MAPS, PTAGIS, Movebank, and ETN that highlight the feasibility of this approach, see the supplemental information online.

Big data from existing monitoring networks possess several valuable properties. They exist for individuals over long durations and across large geographic regions (Figure 1B,C). They include repeated measurements of individual state characteristics such as body condition, age, reproductive status, and parasite loads and/or pathogen presence. Moreover, NEON collects blood, tissue, hair, and fecal samples from a subset of individuals, offering potential for individual genotyping, stable isotope analyses, and hormone assays. Repeated sampling within networks also enables estimates of individual survival. The result is a massive quantity of diverse data that can be leveraged to address key questions regarding the evolution, maintenance, and ecological consequences of behavioral variation and to test hypotheses relating behavioral variation to population- and community-level processes. BBD provides an unrivaled opportunity to understand the ecology and evolution of behavioral variation in an era of global change.

Insights into major outstanding questions

Two main theories have been proposed that explain the existence of intraspecific behavioral variation via ecological drivers (**state-dependent feedbacks**) and evolutionary drivers [**pace-of-life syndrome hypothesis** (POLS)]. These theories have mixed support despite considerable theoretical and empirical attention over the past two decades [2] but may be reconciled using BBD. Adaptive behavioral differences may arise because intrinsic state properties (e.g., body condition, parasite load) and extrinsic state properties (e.g., properties of the social or physical environment) drive positive feedback loops whereby individuals differ in behavior because of state differences, and behavioral variation promotes further state differences (state-dependent feedbacks) [2]. Behavioral variation may also be maintained within a set of coevolved life history, behavioral, and physiological traits that enable individuals with different trait combinations (life history strategies) to achieve similar fitness (POLS) [2]. Quantifying behavior using consistent methods in species and populations under diverse selection pressures is necessary to identify state-dependent feedbacks and the ecological conditions under which they act. Moreover, evidence of genetic correlations between behavior and life history traits would provide strong support for the POLS hypothesis, and among-individual correlations between behavior and life history traits also provide validation. The former could be explored using NEON data, and the latter could be explored with any of the three example networks (Figure 1).

Importantly, BBD provide a means to disentangle the ecological and evolutionary processes that contribute to different types of behavioral variation: among-individual variation (consistent differences among individuals in behavioral averages) and within-individual variation (how consistent the same individual is in repeated expressions of behavior). BBD may also provide the means to identify which behaviors are consistently correlated at the among-individual level (behavioral syndromes), how these axes of behavioral variation should be interpreted ecologically, and which of the proposed **behavioral axes** (such as boldness, exploration, activity, and **sociability**) [2] are conserved across taxa. Finally, BBD provide a powerful tool that can be leveraged to test new hypotheses (Figure 1 and Box 1) and a way to understand how behavioral variation affects biotic interactions.

Extension to population- and community-level dynamics

Understanding ties between behavioral variation and the ecology of species' interactions requires linking repeated

activity, exploration, or sociability. (E) Aspects of individual capture history relative to net hours and capture latency may also be interpreted as indicators of boldness, and spatiotemporal proximity to conspecifics may be used to infer sociability. (F) Movement of PIT (passive integrated transponder) tagged fish is monitored in impeded watersheds using remote detection systems. Activity can be measured using the individual's migration speed (river kilometers moved per hour). Boldness may be interpreted from binary dam passage, passage latency (hours below impediment before passage), and choice of passage type (fish ladder vs. fishway) [13]. Tick and coyote photos by Erik Karits and Alan Emery on Unsplash.

Box 1. A worked example measuring behavioral variation of Chinook salmon

Q: What ecological conditions generate or degrade behavioral variation?

System: PTAGIS – Columbia Basin Watershed (Figure I). Remote detection systems record detections of migrating PIT tagged fish.

Hypotheses and predictions: Impediments to migration of sea run fishes degrade behavioral variation because certain behavioral types are more likely to attempt and/or successfully pass impediments. Behavioral variation should be lower in populations migrating to upper river reaches.

Step 1: Download data using Query Builder 2 in the Advanced Reporting interface (e.g., a query filtering Chinook salmon, *Oncorhynchus tshawytscha*, tagged in 2020 returns 4780 individuals with ≥ten observations [mean, 13.4 ± 7.4 SD]). See Figure II for one individual's mapped observations.

Step 2: Repeatedly measure behavior in the same individuals (e.g., river kilometers moved/h; time below impediment before passage).

Step 3: Group individuals by migration terminus. Partition behavioral variance of each group into its among-individual, within-individual, and residual components using mixed-effects modeling.

Step 4: Estimate a measure of **mean-standardized individual variation** ([2] and references within).

Step 5: Compare variance across groups.

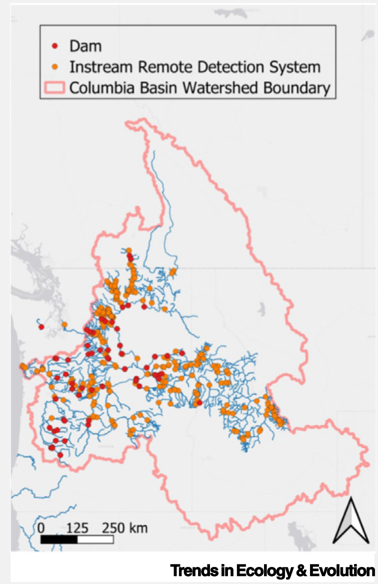

Figure I. Columbia River Basin. Migratory fishes are PIT tagged, and movement throughout watershed is monitored.

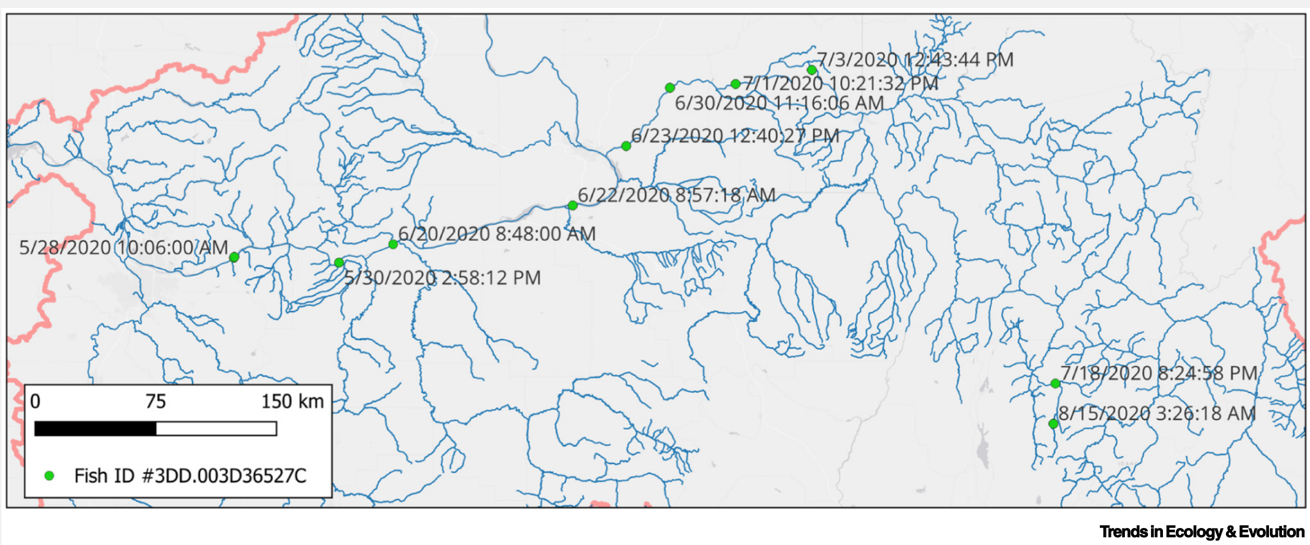

Figure II. Observed detections of one individual tagged Chinook salmon. Note dates are in month-day-year format.

observations of individuals to events that may play out over large temporal and spatial scales. BBD offer novel avenues to resolve this challenge, providing a means to explore the role of among-individual and within-individual variation in affecting competitive interactions, predator–prey interactions, and the interactions that characterize disease ecology [2]. For example, the long-term, large-scale nature of BBD could elucidate how patterns and drivers of animal movements act across scales (a major challenge in movement ecology [7]) as well as provide a means to associate behavioral variation and the transmission of zoonoses that exist across large geographic ranges and involve multiple host species. Additionally, if data on habitat structure exist or can be examined using remotely sensed light detection and ranging (LiDAR) measurements of topographic and/or vegetation structure [11], these metrics offer insight into **resource selection** and **spatial niche specialization**, which may both covary with among-individual behavioral variation [12].

Implications for conservation

A pressing challenge is predicting how individuals, populations, and communities will respond to increasingly variable (and often novel) disturbances [4]. Quantifying behavior from existing large-scale, long-term ecological datasets may make it possible to link behavioral variation to population resilience over large spatial and temporal scales. For example, our perspective enables the use of data collected over critical periods (e.g., extreme disturbance events, species range shifts, invasions, extinctions) to establish baselines to which future studies can be compared, examine behavioral responses to stress, attributes of resilient populations, and early warning signals of at-risk populations. The approach we propose should improve our capacity to forecast future responses to such events [3].

The increased emphasis on big data, long-term ecological research programs, and improved data archiving has led to an abundance of publicly available data, presenting novel opportunities to investigate behavioral variation across broader temporal and geographic scales than ever before. In an era of unprecedented global change, when behavior can be the harbinger of extinction or foreshadow trophic collapse, new perspectives on how to amass BBD are increasingly important. We provide a means to productively leverage large-scale, long-term data to quantify relevant aspects of intraspecific behavioral variation in terrestrial and freshwater systems and offer a perspective on the usefulness of such data for answering major outstanding questions.

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Declaration of interests

The authors declare no competing interests.

Supplemental information

Supplemental information associated with this article can be found online https://doi.org/10.1016/j.tree.2023.08.016.

Resources

[i] https://lternet.edu/
[ii] www.neonscience.org
[iii] http://birdpop.org/pages/maps.php
[iv] http://ptagis.org/
[v] www.movebank.org
[vi] www.lifewatch.be/etn

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