American Society of Naturalists Address

# Where Is Natural History in Ecological, Evolutionary, and Behavioral Science?\*

# Joseph Travis<sup>†</sup>

Department of Biological Science, Florida State University, Tallahassee, Florida 32306 Submitted October 3, 2019; Accepted February 4, 2020; Electronically published May 5, 2020

ABSTRACT: Natural history is the careful observation of nature, wherever nature is. Ultimately, it is what ecological, evolutionary, and behavioral science are supposed to explain. It is difficult to use natural history alone to test hypotheses in these fields because of the complex paths between process and pattern. Few patterns are predicted by one and only one hypothesis, so experiments are almost always necessary. However, the robustness of experimental results depends on how well experimental conditions reflect the integration of natural history. Natural history also plays a vital role in how well we can apply Krogh's principle to our work. Krogh's principle is that scientists begin with an important hypothesis and find a system (organism, habitat, species interaction) with which to test it. However, natural history is essential for knowing whether the question applies to the system or whether we are forcing the question on the system. There is value in beginning one's research not by identifying an interesting question and searching for the right system but by identifying an interesting system in which to ask the right question. This approach carries the danger of parochialism, which can be avoided only by having a command of theory as well as natural history. A command of both areas allows nature to tell us which question to ask instead of demanding that nature answer the question we find most interesting.

*Keywords:* calibrating experiments, experimental realism, hypothesis testing, Krogh's principle, natural history, observational data.

### Introduction

Many years ago, Henry Wilbur and I accompanied the late Joe Bailey on salamander-collecting expeditions in the Blue Ridge Mountains. Our goal was to collect a few individuals of several target species of terrestrial plethodontid salamanders that would be photographed for the field guide that Joe was completing (Martof et al. 1980). At that time, Joe was a 60-year-old full professor, Henry a 30-year-old assistant professor, and I a 23-year-old graduate student. Our typical collecting routine was as follows. Joe decided where we would stop to look for whichever species we were seeking, and the three of us would disperse up the slope to turn rocks and logs to find the animals. I would turn 20 objects and collect five salamanders, of which three would be the target species; Henry would turn 10 objects and collect 10 salamanders, of which nine would be the target species; Joe would turn five objects and collect 15 salamanders, all of which were the target species.

No one who knew Joe Bailey would be surprised that he could collect more salamanders with less effort than anyone else. Joe knew from long experience and careful observation where the best habitat was for whichever species we were collecting, and he knew under which rocks and logs we would most readily find that species. He had field notes, of course, but I never saw him consult them; Joe seemed to rely entirely on memory and intuition.

In that light, if a naturalist like Joe Bailey were to write, "Large flat rocks and decaying downed tree trunks in moist deciduous woods on north-facing slopes at elevations above 900 meters are the preferred habitat for salamander species X," would it constitute a reliable, scientific conclusion about habitat selection in species X? If not, what would be necessary to make it so? Would we want to see quantitative data on the sizes of rocks under which salamanders were found? Would we demand that such data be compared with data on rocks under which salamanders were not found? Would we insist that surveys also be conducted at "control" locations chosen at random with respect to location and elevation? Would we want to see someone else repeat the study to ensure that the results were not an artifact of unconscious bias? Would we insist that these observations and statistical results be linked to a general conceptual issue or theory before we could call our conclusions "scientific"?

The example, while perhaps contrived, leads to an interesting question: What role does natural history play in

<sup>\*</sup> Joseph Travis received the 2011 Edward O. Wilson Naturalist Award. The Wilson Award is given to an active investigator in midcareer who has made significant contributions to the knowledge of a particular ecosystem or group of organisms and whose research and writing illuminate principles of evolutionary biology and an enhanced appreciation of natural history.

<sup>&</sup>lt;sup>†</sup> Email: travis@bio.fsu.edu.

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ecological, evolutionary, and behavioral science? In this essay I will explore this question. It is an exceptionally appropriate subject for an essay by a winner of the E. O. Wilson Award; Ed Wilson led the scientific study of caste polymorphism and ergonomics in ants, island biogeography, sociobiology, and many other topics, yet he entitled his autobiography Naturalist (Wilson 1994). I will argue that natural history, sensu lato, is the foundation of the best ecological, evolutionary, and behavioral science. While this argument may not seem controversial, it can appear to create biased science and run headlong against Krogh's principle (concept first, study system second; discussed below). I will assess this paradox and suggest that our field would be well served if we place more emphasis on letting nature tell us which question to ask instead of demanding that nature answer the question we find most interesting.

#### What Is Natural History?

There are many thoughtful definitions of naturalists and natural history (Greene 2005); I will define natural history as the careful observation of nature (Travis 2009). The careful observation of nature occurs where nature is, whether the intertidal zone of marine waters, the fermenting tissue of decaying fruit, or the environment of an animal's digestive tract. We often think of a naturalist as someone with a deep appreciation for nature, capable of recognizing geological formations, calculating the tides, navigating by dead reckoning, and identifying most organisms in the tree of life at least to the genus level. That person does not exist. For most of us, "deep appreciation for nature" has a bell-shaped distribution centering on a group of organisms, a habitat, or a region we know extremely well, with our expertise diminishing gradually toward environments and organisms that are unknown to us. The important element of the definition is "careful observation," not an a priori definition of "nature."

Compilations of natural history surround us. At the simplest level, we have floral and faunal encyclopedias for specific regions (Weakley et al. 2012; Thomas and Lewington 2016) and, of course, field guides to everything from fungi to fish. At the other end of the spectrum, there is technical natural history, which are articles or monographs focused on a species (Means 2017), a habitat (Vince et al. 1989), or a region (Goebel et al. 2001) that include not only qualitative descriptions but original observational data along with analyses and interpretations of those data in the light of larger concepts or theories.

The reporting of natural history is a continuum from purely verbal to heavily quantitative. Detailed data on the abundance and distribution of species are quantitative natural history. Assays of genetic variation and how it is structured within and among populations are quantitative natural history. Over time, reported natural history has shifted from qualitative to quantitative-compare the description of vegetation associations in Wells (1928) with that in Goebel et al. (2001). We are interested, now, not only in the "typical" observation but in variation. For example, a "typical" observation might be that Brewer's jewelflower (Strepthantus breweri) is found only on serpentine soils (Cacho and Strauss 2014). The variation that strikes us now might be that some species of Strepthanthus are endemic to low-calcium serpentine soils, others are specialists on high-calcium limestone soils, and some are edaphic generalists (Cacho and Strauss 2014). Variation, whether in genome sequences, population densities, the level of edaphic specialization, or mate selection patterns, is natural history and is what the sciences of ecology, evolutionary biology, and behavioral biology set out to explain.

# Can We Use Natural History to Test Hypotheses in Ecology, Evolutionary Biology, and Behavior?

The answer to this question depends on whether there is a unique path from a biological process to a biological pattern. To avoid drifting into needless abstraction, consider a specific example from the past. Anyone who has conducted a census of any group of organisms anywhere can attest that some species are abundant, others common, and others uncommon to rare. A variety of statistical distributions can be fit to these species abundance patterns. Ever since Fisher et al. (1943) and Preston (1948), ecologists have sought to understand which distributions fit which types of communities and why.

One of the more famous of these attempts was Mac-Arthur's (1957) "broken stick" distribution. MacArthur (1957) derived an expected species abundance distribution from first principles. He began with the assumptions that a group of species was dividing a limiting resource, that the amount of resource obtained by each species would reflect an ordered random division of the resource, and that the abundance of each species directly reflected how much of that resource its individuals would obtain. These assumptions led, mathematically, to a particular distribution of species abundance. This distribution was called the broken stick distribution because of the analogy MacArthur used to describe how resources would be divided.

MacArthur's (1957) theory was that species abundances are determined by each species' share of a limiting resource. How might we test this theory? If we use the theory as our hypothesis, then MacArthur's work leads to the prediction that the abundances of species limited by a common resource should fit the broken stick distribution. If we census a community of animals on the same trophic level and the broken stick fits—that is, if our prediction is verified—can we conclude that the species are indeed limited by a common resource? The answer is no, because the statistical pattern of the broken stick distribution can also be generated by models of other processes that do not assume that species share a limiting resource (Cohen 1968).

The point is that, in this case, the same ecological pattern can be the product of two different processes. When this is so, no amount of further observation alone will advance our understanding, and a different approach will be necessary. Lest the example seem archaic, it is worth noting that ecologists continue to argue over interpreting species abundance distributions (Volkov et al. 2005; Chave et al. 2006; McGill et al. 2007). Lest this ecological example seem idiosyncratic, I note that the question of whether there are unique relationships between process and pattern lay beneath the argument over interpreting allele frequency distributions as products of natural selection or genetic drift (Kimura 1983; Gillespie 1991), an argument that has emerged again, albeit in slightly different form (Kern and Hahn 2018; Jensen et al. 2019).

Natural history can be used to test ecological or evolutionary hypotheses in two circumstances. First, it can be used when competing hypotheses about processes generate different unique predictions about patterns. Second, it can be used when a pattern is repeated so often that the collective circumstances in which it appears support only a single hypothesis. Neither circumstance is common. The rarity of the first is primarily a matter of principle; there are few cases of unique paths from alternative hypotheses to distinct unique patterns. The rarity of the second is primarily a matter of practice; it is no easy task to document a compelling case of a pattern that is visible over a wide range of circumstances and that mimics an experimental result (i.e., a particular factor is effective over a range of randomly varying other factors).

Nonetheless, there are successful examples of both uses of natural history. Our diagnosis of the effects of Hurricane Dennis on the genetic population structure of the sailfin molly (*Poecilia latipinna*), a small fish inhabiting coastal salt marshes and tidal creeks, is an example of the first situation (Apodaca et al. 2013). Here we found a striking disruption of the spatial genetic structure of nine *P. latipinna* populations after the passage of Hurricane Dennis. We did not see this same disruption in a simultaneous survey of temporal variation in the population genetics of seven *P. latipinna* populations unaffected by Hurricane Dennis. To bolster the argument, we invoked the unique surge patterns of this storm to explain why the individuals in populations that experienced Hurricane Dennis were scattered and dispersed.

The second situation is illustrated by two studies of character displacement. Dunham et al. (1979) compared gill raker numbers in two species of catastomid fishes in allopatry and sympatry from 182 populations across 20 drainages in 13 US states or Canadian provinces. Dayan et al. (1989) compared skull lengths and canine tooth diameters for two species pairs of mustelid mammals across eight states in the northern United States, from Maine to Alaska. In both cases, the repetition of patterns across many populations and geographic regions represent a situation as close to an experiment (i.e., one factor varying, allopatry or sympatry, all else random) as one can hope to achieve in observations of natural populations.

# How Does Natural History Inform Tests of Hypotheses in Ecology, Evolutionary Biology, and Behavior?

The limits of observation alone in distinguishing competing hypotheses has been the traditional argument for the importance of experimentation, whether experiments are done in nature or in simulacra of nature like phytotrons, artificial ponds, or artificial streams (Bender et al. 1984; Hairston 1989). To produce compelling results, experiments need to be grounded in the natural history of the organisms or the system. While this may seem obvious, "grounding" an experiment in natural history is not always a straightforward matter. All experiments involve artifice; the question is whether the artifice overwhelms the experiment and compromises the interpretation of its results.

The easiest examples to discuss are manipulations of population density designed to test regulation or species interactions. When we conduct an ecological experiment in an artificial setting, have we constructed population densities that are within the range of what we can document in nature (Gascon and Travis 1992; Bassar et al. 2010)? When we manipulate densities in nature to study population regulation, are our manipulations within the range of natural fluctuations (Fowler et al. 2006; Bassar et al. 2013)? There can be virtue in creating a range of densities that include the natural range but extend below and above it, just as there can be virtue in creating extreme phenotypes for studying selection (Sinervo et al. 1992). However, extreme manipulations of population density may offer different information and answer different questions than less dramatic manipulations (see the discussion sections in Fowler et al. [2006] and Ziebarth et al. [2010]). The worst scenario is not knowing natural densities and so not knowing what one's experiment is actually testing.

An analogous situation occurs in the study of social behavior. An individual's social behavior is sensitive to social context, an observation at the root of theory for indirect genetic effects in the evolution of social behavior (Moore et al. 1997). Testing this theory properly requires experiments that replicate the natural composition of social groups. Kraft et al. (2016) used direct observation and underwater video to describe the size and composition of social groups of eastern mosquitofish (*Gambusia holbrooki*) and measure behaviors in the field. She and colleagues then used those results in the design of laboratory experiments testing specific hypotheses about indirect genetic effects in these fish (Kraft et al. 2018).

Grounding experiments in natural history is equally important in evolutionary biology. An accurate separation of genetic and environmental effects on phenotypic variation depends on using natural environments. This has long been appreciated by plant population biologists through their use of reciprocal transplant experiments (Linhart and Grant 1996). When organisms cannot be raised in the wild, using conditions that mimic the salient features of nature is vital for the expression of typical phenotypes (Etges 1993). This is also true for studies of genomic expression. For example, in the cactophilic fruit fly (Drosophila mojavensis) genomic expression patterns in adult female flies depend on host plant (Etges et al. 2015) and development time of larvae (Etges et al. 2016). Raising these flies with excessive artifice-unnatural larval food or conditions that unnaturally prolong development-can produce patterns of gene expression in adults that could prove misleading in studies of adaptation.

Calibrating experimental manipulations to natural history is especially critical when the goal is to compare the relative strength of two complementary factors. For example, El-Sabaawi et al. (2015) used artificial streams to compare the effects of two levels of incident light on ecosystem parameters with the effects of two different phenotypes of Trinidadian guppy (Poecilia reticulata). They were interested in whether the effects of exchanging phenotypes, an evolutionary effect, would be comparable in magnitude to those produced by varying the level of incident light, an ecological effect. They concluded that the difference between two phenotypes was as important in predicting ecosystem parameters as the "bottom-up" effects of light level variation. They calibrated their light levels and the densities of the guppies against what one can measure in nature. It would have been easy to stack the deck, as it were, in these experiments; extreme light level variations might have made light appear overwhelmingly important and the effects of phenotypic variation trivial by comparison.

The unavoidable artifice of all experimentation raises a more subtle issue: Does the experimental protocol itself stack the deck toward a particular conclusion? This has been a long-standing issue in studies of biotic interactions among populations of amphibian larvae (Jaeger and Walls 1989; Gascon and Travis 1992; Skelly and Kiesecker 2001). In this case, the answer depends on which comparison one makes. Skelly and Kiesecker (2001) critically reviewed 227 comparisons from 52 studies and found that laboratory and mesocosm experiments overestimated substantially the effect of interspecific competition compared with field manipulations. On the other hand, within the class of mesocosm experiments, studies of intraspecific competition and predator-prey interactions have produced results that have proven robust to different experimental protocols (Gascon and Travis 1992; Gunzburger and Travis 2005).

Avoiding undue artifice and the guidance of natural history play large roles in discussions of how best to measure mating preferences and preference functions for mate choice in animals (Arnqvist and Rowe 2015; Chenoweth and Gosden 2015; Dougherty and Shuker 2015; Edward 2015; Fitzpatrick and Servedio 2015; Kokko and Jennions 2015; Ryan and Taylor 2015). Kokko and Jennions (2015) pointed out that some assays of mate preference may generate biased results (i.e., "stack the deck"). For example, when individuals are offered a choice between two potential mates and fail to make a choice, the observation is often discarded because the focal individual was sexually unresponsive. However, if a "no-choice" design were to be used, in which latency to mate is used as a measure of preference, then the same focal individual that showed no interest in mating in the other experiment would be included in analyses of this experiment and, because that individual showed little inclination to mate, push the collective results toward an underestimate of the strength of sexual selection. Fitzpatrick and Servedio (2015) and Ryan and Taylor (2015) argued that the best choice among possible tests can depend on what natural history tells us about how and in what context individuals encounter potential mates.

# Does Natural History Properly Inspire Tests of Hypotheses in Ecology, Evolution, and Behavior?

Natural history is what ecology, evolutionary biology, and behavioral biology are supposed to be explaining. Because we, the practitioners of these disciplines, are scientists, we try to infer generalities, identify interesting exceptions, and develop foundational principles. To do so, at least in theory, we identify an interesting conceptual question and then search for a "system" in which to study that question. Like all of biology, we follow Krogh's principle: "for such a large number of problems there will be some animal of choice, or a few such animals, on which it can most conveniently be studied" (Krogh 1929, p. 202). As a result, nearly every grant proposal and every manuscript includes a phrase like "[Your species here] is an excellent system in which to study this problem."

But is it? Does the system actually illustrate the problem, or are we imposing the problem on the system? The ideal match of system to question has two components (Travis 2006): Is the system tractable for the question? Is the question relevant to the system? An answer of yes to the first question is a pragmatic matter; an answer of yes to the second is a matter of natural history.

Let's assume that the first answer is always yes and explore what the second question might really mean. Consider an example modified from Burggren's (2000) essay on model organisms and developmental physiology. We could ask, "How does chronic hypoxia affect embryonic development, and how does the animal cope with chronic hypoxia?" The large embryos and easy laboratory husbandry of zebrafish (*Dania rerio*) make them an excellent system in which to study this question. As it turns out, the native habitat of zebrafish is clear running water that is probably never hypoxic. In this case, the answer to the second question is no. A better choice, at least in fish, might be a species like the pygmy sunfish (*Elassoma okefenokee*), which is found in dense vegetation in warm, shallow, slow-moving water in swamps, lakes, and rivers.

But is *E. okefenokee* a "better" choice? From one perspective, it is in that it likely experiences hypoxia at some points in its life cycle. On other hand, if our question is how a species accustomed to hypoxia differs in response from one that is not, both zebrafish and pygmy sunfish ought to be studied.

Turning to a more controversial question, what if, outside a comparative context, the conceptual question is not relevant to the system? That is, if we are imposing the question on the system, how do we interpret the answer? As an example, consider the elegant experimental studies of stagespecific intraguild predation by Schröder et al. (2009) and Reichstein et al. (2013). These studies examined interactions between Trinidadian guppies (*Poecilia reticulata*) and the least killifish (*Heterandria formosa*), a species endemic to the southeastern United States. Schröder et al. (2009) found that the ability of one species to invade the population of the other depended strongly on relative body size, while Reichstein et al. (2013) showed that habitat complexity did not promote coexistence between the species.

How do we interpret these results? The two species occur on different continents and, in natural populations, occupy slightly different trophic positions (Zandona et al. 2011; Aresco et al. 2015). The experiments were designed to test specific predictions of theory that should apply universally but employed a two-species system to which the question did not apply. To be sure, Trinidadian guppies interact with Hart's killifish (Rivulus hartii) as reciprocal intraguild predators (Fraser and Lamphere 2013), so the question at least applies to guppies if not to the specific interaction with H. formosa. If theory should apply universally, does the choice of species for the testing of it matter? Different readers may answer this question differently. On the one hand, one might argue that, in these cases, the artifice overwhelms the experiment. On the other, one might argue that even if the interaction that was studied was

artificial, the two experiments offer valuable insights into which hypotheses about the stability of size-structured interactions might be more profitable to explore in nature and which might be less so.

What if our research process moves in the other direction? That is, instead of beginning our research by identifying an interesting question and searching for the right system, what if we begin by identifying an interesting system in which to ask the right question. This approach inverts Krogh's principle, stating instead that a particular observation is so interesting that there must be an applicable theory lurking somewhere nearby that one can test with it.

There are two challenges to taking this approach. The first is the potential for contributing to a bias in science. This can happen when one tests a hypothesis in a system where one has reason to expect it to be operating. For example, in the Newport Sulfur Spring in northern Florida, the pulmonate snail (*Physella hendersoni*) is found in only a very restricted portion of the stream, whereas the prosobranch snail (*Planorbella duryi*) is found throughout the length of the stream. I might look at this pattern and propose that interspecific competition is enforcing a habitat distinction. If I find this to be true, was I biased by natural history? Am I contributing to the hardcore meta-analyst's nightmare of nonrandom choice of experimental subjects?

It is not obvious to me that the "inverted Krogh" approach carries any greater risk of bias. If one wants to study interspecific competition and is seeking a system in which to study it, an abrupt transition between species along a gradient would seem an excellent system to use (Hairston 1989; Dunson and Travis 1991). One might even argue that the risk of a priori bias is higher with the Krogh approach because one is actively looking for a natural system that suggests the operation of whatever one wants to study. Different biologists will take different positions on this point; indeed, two distinguished readers of a previous version of this article did just that.

The second, and to my mind more important, challenge is that it might be all too easy to find oneself investigating a parochial problem or one unlikely to produce a novel finding. Let's return to the snails in the Newport Sulfur Spring. Were I to study them, I suspect that I would produce yet another verification of Brown et al.'s (1998) hypothesis about how abiotic factors have different effects on the distribution of pulmonate and prosobranch snails. It is unclear how interesting this result would prove to be to anyone except that beleaguered hardcore meta-analyst.

On the other hand, one never knows because things may not be what they seem. For example, Berger and Kaster (1979) investigated what appeared to be an interesting case of mimicry of a snail by a case-building caddisfly. Anyone familiar with these animals would be struck by the resemblance shown in their figure 1 and probably leap to the conclusion that this reflected mimicry of the snail by the caddisfly to avoid trout predation. Many of us might have stopped at that point and relegated the observation and interpretation to our armory of natural history knowledge. Yet in this case, a series of careful experiments indicated that the caddisflies were not mimicking the snails or, at least, deriving no benefit from the resemblance.

A more recent example is Suetsugu et al.'s (2019) investigation of scent mimicry in a mushroom. In this case, the initial observation in natural history was a distinctive smell like that of fermentation emanating from a mushroom. Careful experimentation revealed this to be a novel and, to date, unique case of mimicry of fermenting fruit by a fungus that functioned to facilitate spore dispersal.

Finally, sometimes the accepted interpretation of natural history is wrong. Longleaf pine (Pinus palustris) once dominated the southeastern Coastal Plain (Wahlenberg 1946). This ecosystem is considered to be maintained in modern times after the introduction of loblolly pine (Pinus taeda) by regular fires that favor longleaf more than loblolly (Wells 1928). Longleaf pine has a distinctive "grass phase" in which the young plant has no aboveground stem and resembles a cluster of wiregrass. In this stage, the plant builds a taproot with stored resources. The plant is resistant to fire because the root collar is kept at the soil surface and the apical meristem of the seedling and young plant is protected by bud scales and the cluster of needles around it (Wang et al. 2016). This stage can last from 2 to 20 years. At some point, when a threshold size has been reached, the tree begins to grow upward with a straight, thin trunk with few, if any, small branches. This growth pattern has often been interpreted as a burst of growth that functions to take the plant quickly through its most vulnerable stage, when the meristem would be exposed to flames of 2-4 feet in height. In fact, I once offered this very interpretation to Ed Wilson on a field trip near Thomasville, Georgia.

The interpretation makes perfect sense within the natural history of the system but is, sadly, incorrect. Experimental work by Wang et al. (2016) showed that (a) the "burst" of growth was not a burst at all but part of a smooth growth curve, (b) there was no evidence for a threshold size that has to be attained before the plant grows upward, and (c) the growth pattern of fire-resistant longleaf was very similar to that of fire-susceptible loblolly. Moreover, there was no evidence that longleaf plants in this stage had higher survivorship than expected from a typical sizeat-age vertical life table.

If a student came to us wishing to pursue any of these initial observations, I suspect that few of us would have been encouraging. After all, if the caddisflies were mimicking snails, it would be yet another in a long line of examples of Batesian mimicry. If the odor of the mushroom had no discernible significance, there would be no story to tell after a great deal of work. If the longleaf pine saplings did grow in a burst that enhanced survival, we might catalogue it as one more example of the life-history theory that revolves around minimizing the ratio of mortality rate to growth rate (Werner and Gilliam 1984).

Perhaps the danger of parochialism is why we train our students to follow Krogh's principle-to begin with an important question and then identify a system in which to study it. However, parochialism is not an unavoidable consequence of inverting Krogh's principle. For example, the natural history of ants in Melanesia, their taxonomy and geographic distribution, led Wilson (1961) to formulate the theory of taxon cycles, which led to the broader theory of island biogeography (MacArthur and Wilson 1963). I suspect that for most of us, our work reflects a balance between following Krogh's principle and following natural history where it leads, which is what I will call Ketterson's principle (Ketterson 2020). Reflecting on my own work, I can identify articles whose origin absolutely followed Krogh's principle (Redmond et al. 1989; Gascon and Travis 1992) and some whose origin followed Ketterson's principle (Travis 1984; Apodaca et al. 2013). Most of my work has emerged from a combination. On the one hand, I carried familiarity with the natural history of many organisms; on the other, I carried conceptual questions that interested me. I have spent my career attempting to match them well, an approach that I might call Greene's principle (Greene 2005).

The critical issue in any approach to ecology, evolutionary biology, and behavior is understanding the implications of the word "identify." To identify a system in which to study an interesting problem well, we need to know a lot about the system. To identify an interesting question to ask with any system, we need to know a lot about concepts and theory. Without both sets of knowledge, we risk a gross mismatch between system and question. To paraphrase Wilbur (1972), without theory, our data are unlikely to be interesting; to add to that notion, without natural history, our questions are unlikely to be useful.

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