

Models on the Runway: How Do We Make Replicas of the World?*

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ABSTRACT: Models are universal in science, both as theoretical formulations of reality and as model systems, representatives of other organisms. A recent paper on how scientists view the world divides our work into the mind, the lab, and the field and suggests that models must not be conflated with reality. But in practice, these distinctions are blurred. For example, are flour beetles a model system for other insects when their natural habitat is the same as the way they live in the lab? In addition, models can become restrictive when they are viewed as archetypes, making us overgeneralize about the world and ignoring meaningful variation. The study of sexual conflict in insects illustrates some of the pitfalls of relying on *Drosophila* as a model system for sexual selection. Microbes can be used as models for populations and communities and are essential parts of larger biological systems. Finally, some models are not meant to replicate the world but are worlds unto themselves in which diverse possibilities can be directly observed.

Keywords: model, proof of concept, theory.

Introduction

Models are universal in science, and ecology and evolution are no exceptions. We use models in many senses. They can be replicas, in the way that model airplanes are miniature versions of the real thing; for biologists, this use means that models imitate nature. They can be theoretical abstractions of natural processes, with general rules that could govern a variety of systems. They also can be their own internally consistent reality, without reference to any particular spe-

cies or ecosystem. Finally, we also employ what might be thought of as models of convenience: *Drosophila*, *Caenorhabditis elegans*, or *Arabidopsis*. These are still models, even though they are actual species or systems—not equations or verbal constructs—and we treat them as stand-ins, representatives of others in their class. As Seger and Adler (2002) wrote, “Any formal device that facilitates ‘what if’ reasoning can be called a model” (p. 684).

Although models have a variety of functions, scientists sometimes make the mistake of assuming that the point of constructing them is that they eventually will be tested using a particular system and that models, particularly mathematical models, are not useful unless it can be demonstrated that the model is consistent with the real world. However, many models are not intended to represent nature. As Seger and Adler (2002) note, “Models in evolutionary biology, by contrast, are not hypotheses to be tested for possible acceptance as descriptions of reality” (p. 684). In this sense, biological models are not special; they can be thought of in the same way as, for example, fashion models, an analogy that may not be immediately apparent. While Seger and Adler (2002) suggest that fashion models show “how the viewer might (with dieting) appear to others if wearing the same clothes,” we think this is not quite correct. Although, of course, they are human beings, fashion models are conceptual, having more in common with theory by conveying an emotion or a set of abstractions than with replicas or model systems such as *Drosophila*. Clothing designers do not imagine that the average person will wear the actual clothes demonstrated on the runway any more than researchers using fruit flies believe that their results will apply in the finest detail to every other organism. Instead, the concept behind a given style is extended into items that eventually appear on the rack, much altered from the original, to be worn by people other than the idealized forms of the people who demonstrated them. In both cases, the mistake of overgeneralizing can lead to problems, as we discuss in the section on model systems below.

The distinction between kinds of models is reflected in another division that ecologists and evolutionary biologists

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have been concerned about for many years: the gaps between theory, laboratory experiments, and fieldwork. Robert Kohler's (2002) book *Landscapes and Labscapes* traces these boundary issues in the early to middle-twentieth century, when natural history became science, following the idealization of Darwin as a hero who "showed how backyard phenomena could reveal evidence of natural selection" (p. 33). Kohler (2002) goes on to note that the glamour, such as it was, of natural history began to fade in the early 1900s, as supposedly more rigorous physiology and botany—with an emphasis on laboratory experimentation and methods—became popular in universities. Whether one practiced ecology and evolutionary biology in the field or performed experiments in the laboratory became a litmus test of legitimacy for scientists, and the latter was viewed as clearly superior (Kohler 2002). Scientists who moved from the field to the lab were seen as making progress, in stark contrast to those who attempted the reverse. Arguably, modern-day researchers are dogged by similar perceptions, particularly as fast-moving areas such as genomics attract headlines (Travisano and Shaw 2012; Zuk and Balenger 2014).

At the same time, some ecologists and evolutionary biologists in the early to mid-twentieth century continued to argue for the relevance of field studies. Francis Sumner, for example, examined adaptation in *Peromyscus maniculatus*, comparing coat color in mice collected from different habitats as well as rearing them into the laboratory. He never gave up on combining the two approaches, and in Kohler's (2002) words, "his experiences in both field and lab gave him confidence that field observations were as likely as any experiment to reveal how evolution worked" (p. 145).

How dissimilar are the lab, field, and theory and how are models used in all three approaches? Here, we reconsider different types of models and their uses, paying particular attention to the use of microcosms and arguing that replicating nature is not an important or even desirable goal. Finally, we discuss how theoretical or mathematical models are more similar to model organisms or model systems than had previously been recognized.

Verbal versus Mathematical Models: Simple Is as Simple Does

Verbal models have almost always preceded empirical investigation, and in the past several decades mathematical models are increasingly generated as well. Many of the same criticisms can be and have been made about both verbal and mathematical models, and understanding the relevance of each provides a broader appreciation of the utility of modeling. Verbal models have a long history in organismal and population biology, with both positive and negative associations (Peters 1991; Pigliucci 2013). For example, verbal mod-

els can be difficult to formulate for complex relationships (Salt 1983), leading to oversimplification and introducing ambiguity (Grimm et al. 2006; Pianka 2011), thereby causing errors in prediction (Loehle 1988) and fruitless debate (Hunt 2007). Examples include models of good genes sexual selection (Kokko 1998), speciation (Gavrilets 2010), and even of the value of theory itself (Scheiner 2012). Nevertheless, verbal hypotheses are usually the first step in model building (Johnson and Omland 2004; Restif et al. 2012), providing the rationale and broad outlines for subsequent model development (Schneider 2009).

These different views of verbal models arise from how they have been used and misused. At their best, verbal models are a powerful motivation for research (May 1981). They can provide a coherent justification for the value of a research direction and for specific modes of investigation. They provide especially powerful "how possible" explanations, bringing together diverse phenomena and observations, whose linkage is uncertain and remains open for interpretation. By and large, these explanations are about developing a line of thought on plausibility: how might something be explained. Verbal models are valuable under these circumstances partly because of their indeterminism: functional relationships remain uncertain and are often unstated, so that a general idea is not constrained to one set of circumstances. By suggesting possibilities, researchers can gain insight on the topic to be explained: what an explanation might look like and what is likely to be important. "How possible" explanations are helpful in distinguishing potentially fruitful avenues of investigation from those that are less likely to yield informative results. Verbal models can specify cause and effect and leave precision open for interpretation and investigation. The most well-known verbal model in biology is that provided by Darwin in *On the Origin of Species* (Reiss 2007; Pigliucci 2013), which famously did not specify a mechanism for trait inheritance. It was assumed that there was such a mechanism, for the sake of development of the model. Darwin's focus was on articulating how natural selection provided an explanation for the diverse biological phenomena that were already known and was transformative in changing perspectives on their interpretation.

The downside of verbal models occurs when "how possible" explanatory power is invoked as a definitive explanation, becoming essentially a "just so" story. Because verbal models necessarily leave out precision and often specificity, important flaws may not be apparent, especially those involving jumps or errors in logic (Clements 1916; Hoffman 1979). These limitations are often partially addressed using mathematical models, which fill in some of the details left out of verbal models through the elaboration of specific and precise relationships. As in verbal models, mathematical models typically involve important assumptions, but also as in verbal models, the goal is not necessarily in identifying

critical assumptions for their subsequent testing. Rather, the goal can be to further a line of “how possible” reasoning, and it is on this aspect that some mathematical models are frequently misunderstood. Instead of being better approximations of reality, mathematical models can act as proof-of-concept tests of the logic in verbal explanations (Servedio et al. 2014). They lay bare the assumptions on which theory rests and then determine quantitatively whether, given the assumptions, a particular explanation is plausible. While such mathematical models may yet trade off precision against generality, the focus is on possibility.

Early theoretical population genetics exemplifies the transition from verbal to mathematical modeling. The mathematical framework provided by Fisher, Haldane, and Wright in the 1920s and ’30s is largely devoid of direct evidence for the mechanisms of inheritance or gene action (Provine 1971) or, initially, even of the basis for genes. Rather, early population genetics mathematizes Mendelian inheritance and natural selection, without actually requiring a specific material basis for inheritance (Wright 1931), which again was assumed for the sake of model development (Provine 1971). Genes and the particulate basis for inheritance were mathematical constructs that were tremendously useful in understanding inheritance and predicting the outcomes of crosses and inbreeding. In much of the initial modeling, very little of the complexity of biological systems is included. For example, discussions of Hardy-Weinberg equilibrium often provide a long list of assumptions of biological factors that are absent from the mathematical model (Waples 2015). In contrast, the list of factors included in the Hardy-Weinberg equation itself is far shorter, in large part because it is an idealized proof-of-concept model, one that provides a “how possible” explanation for allele segregation.

With technical advances in molecular biology and increasing knowledge of the material basis of biological mechanisms, such “how possible” approaches have become somewhat less common: Why imagine how a phenomenon might occur when it can be directly investigated empirically (Begun et al. 2007; Harpur et al. 2014)? But the value of these modeling approaches persists, in large part because of the richness and complexity of biological systems. The recent realization that organismal and population biology has some of the complex dependencies of ecosystems is leading to a resurgence in “how possible” modeling approaches in those subdisciplines (Solopova et al. 2014; Forsman 2015; Linnquist et al. 2015). Using these approaches, specific ecological or evolutionary factors are the focus of investigation and the underlying basis for the factors is abstracted, even when this basis is understood (Caswell 1988). For example, the evolution of social behavior can be modeled without referring to its specific benefits (Nowak and Coakley 2013).

The goals of such a model do not involve assumptions associated with the abstracted biological details or identi-

fication of specific causal loci, which can be surprising to some researchers given the current emphasis on increasing realism by leveraging computational resources. For example, Servedio and Burger (2015) investigated the effects of sexual selection on trait divergence using a model with a two-locus system for traits and preferences, linkage, and the typical combination of evolutionary processes involving migration and selection. They state,

The very simple models of assortative mating considered in this article are not meant to match specific cases in nature, but instead to isolate the effects on trait divergence of the sexual selection generated by phenotype matching and preference/trait mechanisms. It thus becomes possible to better understand the causes of the underlying dynamics of more realistic, and hence more complicated, biological scenarios. (Servedio and Burger 2015, p. 2659)

Thus, by emphasizing simplicity, mathematical models can provide insight on complex systems without directly modeling the complexity (fig. 1). Mathematical abstraction of complex systems provides researchers absolute control of the study system and the ability to focus investigation on specific factors to the complete exclusion of others not of current interest. Mathematical models are eminently tractable and far more easily manipulated than the reality they represent, and multiple simple mathematical models can be used to investigate different aspects of reality. Lab models are intermediate in virtually all respects, less controllable than mathematical models but also including more of the complexity. This one-dimensional view is illustrated in figure 1 and is often implicit in the way that models are

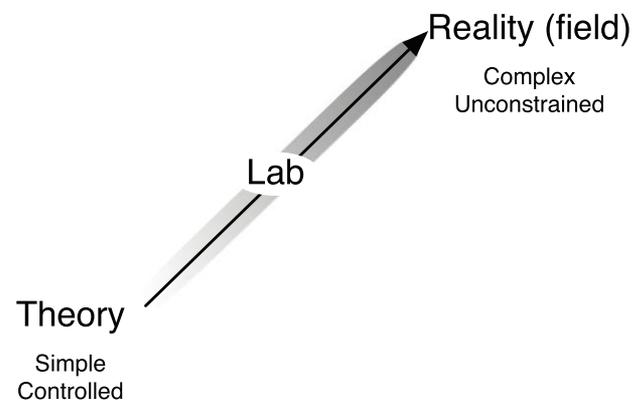


Figure 1: Theoretical models can be useful because of the insight gained by simplicity and exclusion of extraneous complexity. Laboratory models gain some of these benefits and incorporate some of the complexity of field studies.

incorporated into ecology and evolution research, but as we discuss below, it also has serious limitations.

The Lab, the Field, and Theory: Separate but Equal? Or Equally Inseparable?

Sumner's optimism in the early twentieth century about the usefulness of field experiments notwithstanding, the idea that lab and field are at odds—and that both are at odds with a theoretical approach to science—has never gone away. In one of the more recent considerations of this division, this time by philosophers of science, Winther et al. (2015) say, “Scientists use models to understand the natural world, and it is important not to conflate model and nature” (p. 12). They are eager to differentiate studies of theoretical, lab, and field populations and use classic examples (R. A. Fisher's examination of effective population size, Park's *Tribolium* competition experiments, and Lack's studies of Darwin's finches) to bolster their argument.

We are not so convinced that models and nature are separable, either in the lab, the field, or the equation. Below we explore the division between laboratory, field, and nature that Winther et al. (2015) cite, noting the porous boundaries among the three areas. Kohler's (1994) excellent book *Lords of the Fly* explores the making of a classic model system, *Drosophila melanogaster*; we suggest that the vagaries of history and tradition, in addition to incidental aspects of an organism's biology, may have influenced the establishment and use of other model species as well.

Take, for example, the flour beetles in Park's famous studies. They were studied in the laboratory, to be sure, rather than the wilds of the savannah, and hence Winther et al. (2015) firmly classify them as such. But for the *Tribolium* themselves, the distinction may not be so clear. Flour beetles are stored product pests, and they have been commensal with humans for thousands of years (Shapiro 2013), whether in clay urns or Tupperware containers. What is their natural habitat? They do not exist in the wild, exactly, or to be more precise, their wild habitat and their laboratory or experimental one are one and the same. Certainly, in the laboratory, the food supply, temperature, population density, and so on can be manipulated by the investigator, but these elements also vary of their own accord. The distinction between lab and field is blurred in this situation, and it is not clear to us what is gained by insisting on the demarcation. Indeed, such discussions are reminiscent of environmentalists' considerations of what “wilderness” really is and how it influences our views of nature (Cronon 1996).

Even more blurring of boundaries appears in another quintessential model animal, the laboratory mouse (*Mus musculus*), a workhorse for biomedical research. Yet these animals, too, have a life in “nature,” and it is worth considering which one is the replica—and of what. Like flour

beetles, house mice, as their name suggests, have been commensal with humans for millennia, and they have also been used as experimental laboratory animals for many decades. Their lives in laboratory cages are, of course, quite different from their lives in barns and other human constructions.

For the last several years, Wayne Potts and colleagues have been studying laboratory strains of mice under field-like conditions, with individuals able to move and interact in populations that approximate those in nature. One such study compared the fitness of inbred mice obtained through sibling mating and outbred house mice in barnlike enclosures (Meagher et al. 2000). Although inbreeding has relatively little effect on reproductive success in laboratory populations, under the field conditions, inbred males' reproductive success was up to eight times lower than that of the outbred individuals (Meagher et al. 2000). Based on their observations of the mice, the researchers suggest that the inbred males probably had a much harder time maintaining territories. They also note that their estimates of fitness were conservative, because the females in their study did not have to compete for food or nest sites (Meagher et al. 2000).

In another study from the same group of scientists, mice were fed mouse chow that had 25% of its calories derived from high-fructose corn syrup, an amount of sugar comparable to three cans of soda per day for a human (Ruff et al. 2013). The mice, along with controls, were transferred into the barn at 26 weeks of age, and their survival and other characteristics were monitored. The mortality of the experimental females was twice that of the controls, an effect size that surprised even the investigators, who commented, “By almost every metric, they are perfectly fine in cages . . . but in the semi-natural environment, with competition between experimental and control animals, we see this large difference.”¹

Do these results mean that lab mice are a good model system or not? From our perspective, the point is not that inbreeding is worse than has been believed, or that high-fructose corn syrup is dangerous to our health and should be banned (though both may be true), or that we should stop using laboratory mice in biomedical or nutrition research. It is that what we term representative, or universal to allow generality, is more context-dependent than we may have thought. Models may be models in some environments and not others. The line between model system and nature, and between a theoretical model and the real world, is far more blurred than is often recognized. We are not sure what the solution is—surely not to stop using laboratory rodents—

1. The quotation comes from a Why Files commentary on Ruff et al.'s (2013) work, “Sugar: A Bitter Flavor?” posted on Aug. 5, 2013: <https://whyfiles.org/2013/sweet-and-sour/index.html>.

but we think the questions raised by these context-dependent results have not been fully considered.

It could also be argued that findings that are robust to both controlled (laboratory) conditions as well as the more variable conditions of the field should be more trustworthy, because the consistency indicates greater reliability. Although we applaud the use of both settings by biologists, we are not convinced that this principle necessarily holds, since some perfectly valid results might be simply too difficult to demonstrate under one set of circumstances or the other.

Studies with microcosms (ecosystems with defined boundaries) exemplify the challenges of making precise distinctions between laboratory and field, and in drawing general conclusions from experimental results. There is a long history of investigation with microcosms, some of which was foundational in early ecological and evolutionary thinking (Gause 1934). The merits of microcosm studies largely involve control; they inherently harbor less uncontrolled variation in both biotic and abiotic factors than would be found. These benefits of control—the ability to exclude the effects of some factors and systematically explore others (Hurlbert 1984)—do not mean that control is necessary, desired, or possible for all factors. The only necessarily controlled aspect of a microcosm study is that there are microcosms, whether they occur in natural or laboratory settings (Heemsbergen et al. 2004; Srivastava et al. 2004). The fuzzy boundary between field and laboratory models is traversed by increasing amounts of control.

One of the benefits of controlled experiments is the ability to “simplify nature so that it can be more easily understood” (Jessup et al. 2004, p. 191). Complex systems can be difficult to disentangle and thereby determine cause and effect, while simplified systems limit the number of possibilities to a few that can be investigated. Another benefit of controlled experiments is that they can be complex and yet understandable, building on the results of prior studies. Greater environmental variability, genotypes, and species can be added, whose interactions can be understood in light of the more simplified systems. This approach is implicitly already used, even in the simple experimental studies, as virtually all biological model systems are inherently complex. DNA replication, cellular metabolism, and protein synthesis involve the coordinated activity of hundreds to thousands of genes, all of which are sufficiently well understood so that they can be black-boxed, at least temporarily, when investigating organismal or population-level processes. With advances in understanding simplified systems, additional complexity can be added (Harcombe et al. 2016) and black boxes opened (Dean et al. 1988; Meyer et al. 2016).

Does recognition of control in field and lab studies help distinguish between theory and the real world? Laboratory

microbial experimental evolution is in some ways the most extreme type of controlled microcosm study. Replicate populations of hundreds to billions of organisms are incorporated into experiments at modest cost, aiding investigation of population and evolutionary processes and dynamics (e.g., Tenaillon et al. 2016). Most studies have involved extensive control (Bell 1997). The abiotic environment is tightly controlled for temperature, structure, and added resources. The biotic environment is typically limited to only those species included at that outset and, initially, to specific genotypes or strains. Because of this, the experiments have not included substantial ecological complexity and thus may appear to suffer from a lack of biological realism. However, what they provide are much of the same benefits as that from the transition from verbal to mathematical modeling: extending the line of “how possible” reasoning. Microbial experimental evolution studies act as proof-of-concept empirical extensions of verbal and mathematical models. One might ask how sexual reproduction is evolutionarily beneficial (Zeyl and Bell 1997; Goddard et al. 2005), historical contingency shapes evolution (Blount et al. 2008), or multicellularity originates (Ratcliff et al. 2012; Driscoll and Trivisano 2017), among many possible questions (Garland and Rose 2009; Kassen 2014). Like some verbal and mathematical models, microbial selection experiments are generally not meant to match specific cases in nature. Rather they stand on their own, as worlds unto themselves.

The perspective of Winther et al. (2015) distinguishing between studies of theoretical, lab, and field populations is a useful reminder to researchers to consider strengths and weaknesses of different modeling approaches, particularly in evaluating the scope of their results. However, we perceive model systems as differing as a matter of degree rather than kind (fig. 2). In part, this is because of advances in understanding biological systems, allowing results to be contextualized along a gradient of complexity rather than binned as “laboratory” and “field.” It is also due recognition that model simplicity and control are not necessarily co-determined, thereby making possible a much greater range of exciting potential model systems.

Model Systems and Theoretical Norms

Model organisms or systems are not always thought of in the same way as theoretical models, but they share many attributes. Both are idealized versions of the world, intended to create generalizations that can be applied to many systems. Both struggle with how much complexity they can include (Creager et al. 2007). And with both, we run the risk of over-extending those generalizations. This danger is not new; Beach’s (1950) classic paper “The Snark Was a Boojum” exhorted psychologists to embrace a larger variety of test subjects than rats and pigeons, but while his work is widely cited,

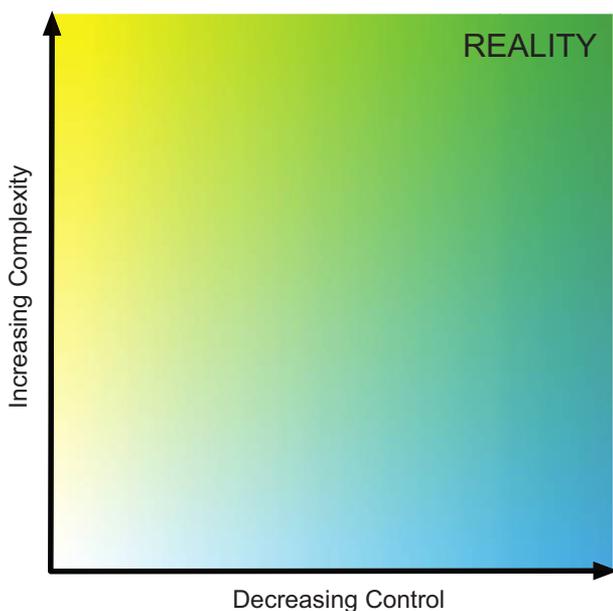


Figure 2: Model complexity and control are not necessarily linked and can be uncoupled with conceptual and technical advances.

the reliance on a few model organisms both in psychology and beyond has continued unabated. Nonetheless, as the title of Bolker's (2012) commentary in *Nature* warns, "There's more to life than rats and flies" (p. 31).

Such a focus on just a few model organisms can lead us astray, partly by making us think biology is more homogeneous than it is, with all mammals like rats and all insects like *Drosophila*, and partly because selection in the laboratory can produce unintended side effects. For example, if researchers tend to choose rats less inclined to bite their handlers, then understandably enough, more docile individuals will come to dominate the animal rooms of research institutes and universities. But what if aggression is linked to the response to a drug or the rate of muscle development in response to exercise? Such inadvertent correlations might then color the results obtained and make our understanding of biological function narrower.

These difficulties are not limited to biomedical research. Although ecologists and evolutionary biologists use a wide range of study organisms, certain fields may still have an overreliance on a few model systems. In turn, those model systems can become normative, even prescriptive, so that it is assumed that what occurs in barn swallows, *Daphnia*, or *Drosophila* is the expected way of performing, whether in reference to physiology, genetics, or behavior. As Ankeny and Leonelli (2011) observe, model organisms are useful insofar as their qualities are conserved through evolutionary time, but they can become idealized, even to the point of being viewed as archetypes.

This difficulty of overgeneralizing is linked to another problem in ecological and evolutionary research: taxonomic bias. Conservation biologists, for example, have long decried the focus on charismatic megafauna as targets of preservation, sometimes at the expense of less glamorous but equally deserving species (Clark and May 2002). In other areas, a focus on a few organisms can foster confirmation bias, in which we are most likely to notice only those findings that confirm ideas we already hold and ignore or discount the rest. *Drosophila*, for example, has been used as a model system in sexual selection for decades, and when sexual conflict became a topic of interest, it was natural to continue using the flies as subjects. Indeed, many exciting discoveries about antagonistic selection have been made using *Drosophila*, such as the finding that males produce toxic substances in their seminal fluid that reduces female fitness (Chapman 2001). But how representative of all insects, let alone other animals, are the flies? A survey of literature on sexual selection in insects revealed that *Drosophila melanogaster* was used in more than one-quarter of sexual conflict research over the past few decades (Zuk et al. 2014). It may well be, however, that other species differ considerably from them in many respects, including the degree to which male and female interests diverge during mating, making the dominance of just a few species in the sexual selection literature problematic (Zuk et al. 2014).

Role Models and Male Model Systems

Model systems, of course, are not studied for their own sake; we seek to generalize by using, as mentioned above, species with representative characteristics. But when does "representative" become "normal"? And further, what if we use our model systems as if they were role models, which are explicitly intended to be emulated?

A sometimes-overlooked place where we may have accepted a model system—and potentially turned it into a role model—is the use of males as subjects. For centuries, people have used the male as a generic, whether in language or as biomedical research subjects. This tendency has extended to our view of which gender more appropriately represents science; scientists are usually visualized as male by students, evidenced by the Draw-A-Scientist Test, which continues to show a male bias as it has since its inception more than three decades ago (Chambers 1983; Steinke et al. 2007). Scientists are also usually depicted as male in other media, including advertisements and illustrations, even those in scientific publications (Barbercheck 2009).

Since its inception, biomedical research has relied mainly on male subjects, whether human or nonhuman, which meant that recommendations for treatment based on such research did not always apply to all genders (Beery and

Zucker 2011). This issue has been recognized as a problem for quite some time; in 1990, the National Institutes of Health (NIH) established its Office of Research on Women's Health, followed by the 1993 NIH Revitalization Act, PL 103-43, which directed the NIH to establish guidelines for inclusion of women and minorities in clinical research. The problem has persisted, and in 2014, the NIH announced a requirement for grant applicants to balance sex of animals and cells they intend to study, a mandate that biomedical researchers are working to incorporate into practice. Yoon et al. (2014) examined major surgery journals for the use of male or female subjects in cell lines or experimental animals. The studies were overwhelmingly male-biased, leading the authors to conclude that "sex bias, be it overt, inadvertent, situational, financial, or ignorant, exists in surgical biomedical research" (Yoon et al. 2014, p. 508).

In an example more in keeping with ecology and evolutionary biology, animals—including those from the female-dominated societies of the eusocial insects—are usually referred to as male, whether in the media or the classroom (Zuk 2002). Such an assumption overlooks the often unique contributions of females and risks missing the diversity of the natural world.

We argue that all these usages present males as, in effect, a model system, a representation of a kind. Just as we need to be concerned with our use of theoretical models and whether we overextend their generality, we need to consider how a focus on males can limit the generality of our work. When we see males as the generic, the norm, we miss the variation that is an essential part of nature. Females become an afterthought, something to study only after we understand the model system itself.

Conclusions: Why Models—and Model Systems—Matter

Models, and model systems, are here to stay, of course. But they are increasingly set apart as if their use is an industry unto itself, with its own rules and reasons for existence. We suggest instead that models and the real world are simply parts of a continuum rather than separate entities. Models can tell us what is normal—at least for some situations—and natural, whatever that means. They can show us what is possible, but they are not goals to be emulated, so that deviation from the model system becomes suspect. They can reveal our biases as they caution us about overgeneralizing. They do not need to be tested against reality to be meaningful.

We are especially excited by the potential for models to be unshackled from the rigid perspectives dividing theory, the lab, and the field. We gain by the ability to interpret results without a strict boundary between artificial and natural, a distinction largely without merit in the anthropo-

cene. One of the challenges in current biological research is assimilating the increasing amount of information about biological systems. Leveraging this body of knowledge to improve understanding across levels of biological complexity is largely an unrealized opportunity. In part, this is due to a lack of varied perspectives on the different model systems utilized by researchers. Rigid boundaries on what can be learned from various model systems unnecessarily limit interdisciplinary explanation, a limitation that is avoided by having a more nuanced perspective of such systems. Integration of results across model systems is facilitated when they are not perceived as conceptually distinct approaches that are unconnected with one another.

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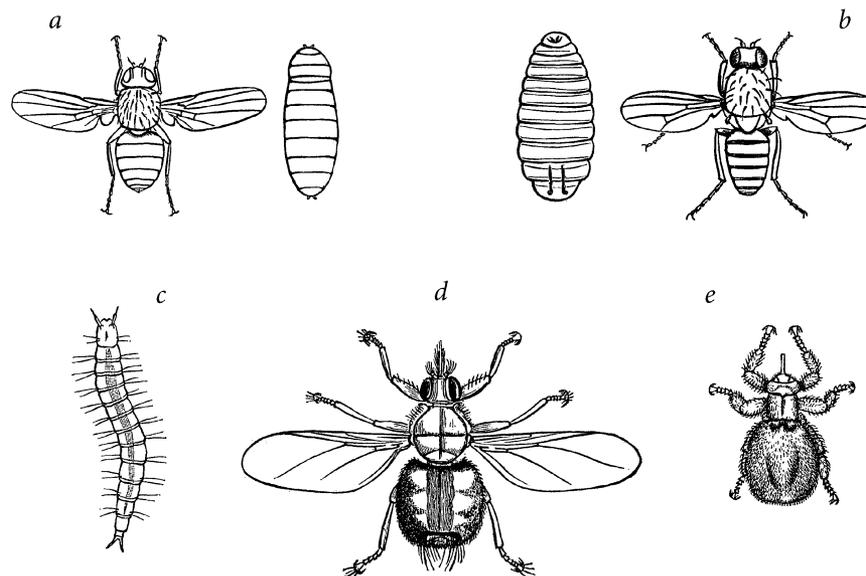
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“I have frequently found the pupæ in the bottom of barrels in a cellar in the winter, and the flies appear in the spring. In the early apples, the larvæ work about in every direction. If there are several in any apple, they make it unfit for use. . . .’ Baron Osten Sacken informs me that it is a *Drosophila*, ‘the species of which live in putrescent vegetable matter, especially fruits.’” Figured: a, “a small black fly . . . which Baron Osten Sacken refers doubtfully to the genus *Lonchæa*”; b, “the rather rude figures of the larva . . . and puparium . . . of the *Musca domestica* of Europe”; c, “the Flea”; d, “the Bird-tick, *Ornithomyia*”; e, “the wingless Sheep-tick, *Melophagus ovinus*.” From “A Chapter on Flies [concluded]” by A. S. Packard Jr. (*The American Naturalist*, 1869, 2:638–644).