Per Aspera ad Astra: Through Complex Population Modeling to Predictive Theory

Author(s): Christopher J. Topping, Hugo Fjelsted Alrøe, Katharine N. Farrell, and Volker Grimm

Source: *The American Naturalist*, Vol. 186, No. 5 (November 2015), pp. 669-674
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/10.1086/683181

Note

Per Aspera ad Astra: Through Complex Population Modeling to Predictive Theory

Christopher J. Topping,[1,*] Hugo Fjelsted Alrøe,[2] Katharine N. Farrell,[3] and Volker Grimm[4]

1. Department of Bioscience, Aarhus University, Grenåvej 14, 8410 Rønde, Denmark; 2. Department of Agroecology, Aarhus University, Blichers Allé 20, 8830 Tjele, Denmark; 3. Institute of Environmental Science and Technology (ICTA), Autonomous University of Barcelona (UAB), Edifici C–Campus de Bellaterra, 08193 Cerdanyola del Vallés (Barcelona), Spain; and Division of Resource Economics, Albecht Daniel Thaer Institute of Agriculture and Horticulture, Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany; 4. Department of Ecological Modeling, Helmholtz Center for Environmental Research (UFZ), Permoserstraße 15, 04318 Leipzig, Germany; Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, 14469 Potsdam, Germany; and German Center for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

Submitted April 28, 2014; Accepted June 10, 2015; Electronically published September 29, 2015

abstract: Population models in ecology are often not good at predictions, even if they are complex and seem to be realistic enough. The reason for this might be that Occam's razor, which is key for minimal models exploring ideas and concepts, has been too uncritically adopted for more realistic models of systems. This can tie models too closely to certain situations, thereby preventing them from predicting the response to new conditions. We therefore advocate a new kind of parsimony to improve the application of Occam's razor. This new parsimony balances two contrasting strategies for avoiding errors in modeling: avoiding inclusion of nonessential factors (false inclusions) and avoiding exclusion of sometimes-important factors (false exclusions). It involves a synthesis of traditional modeling and analysis, used to describe the essentials of mechanistic relationships, with elements that are included in a model because they have been reported to be or can arguably be assumed to be important under certain conditions. The resulting models should be able to reflect how the internal organization of populations change and thereby generate representations of the novel behavior necessary for complex predictions, including regime shifts.

Keywords: complexity, error avoidance, agent-based models, model development, modest approach.

Introduction

In this note, we challenge the central dogma of ecological modeling that for developing theory, keeping models simple is always more important than making them realistic. The emphasis here is on "always," as there are different kinds of models. We focus here only on those models that are designed to represent systems and their functioning, not just ideas.

* Corresponding author; e-mail: cjt@dmu.dk.

Am. Nat. 2015. Vol. 186, pp. 669–674.
DOI: 10.1086/683181

Roughgarden et al. (1996) introduced the distinction between minimal models for ideas and minimal/synthetic models for a system. Models for ideas are developed for exploring general concepts across systems, such as density dependence, competitive exclusion, competition/dispersal trade-offs, and stabilizing mechanisms. They indeed have to be as simple as possible, and they are not designed for making specific, testable predictions. In contrast, models for a system are more tailored to specific systems or classes of systems. Here, the intended potential for making testable predictions is an important modeling design criterion.

Models for a system—in particular, synthetic models—are now widely used in ecology; synthetic models synthesize submodels representing small spatial units and/or individual organisms into realistic models of populations, communities, or ecosystems. However, their predictive power is often still limited, and to date no general, predictive theory seems to have emerged, despite the high hopes of the pioneers of this kind of modeling (Huston et al. 1988; DeAngelis and Mooij 2003; but see Stillman et al. 2015). We believe that this slow progress is, to a large degree, due to uncritically transferring the paradigm "as simple as possible" from minimal to synthetic models. Synthetic models, which are usually implemented as simulation models, come with a price: they are hard to develop, understand, and parameterize (Grimm 1999). But our main point (as indicated by the Latin phrase in the title, which means "through hardships to the stars") is that to reach the stars, predictive models and associated theory may require adding still more complexity to our models for a system.

We first discuss and exemplify the important and to date widely ignored distinction between two different types of errors modelers try to avoid, which we here dub "false inclusion" (a factor is included in a model even though it is not essential for the model's purpose) and "false exclu-

sion" (a factor is excluded even though it is sometimes important). We then discuss why traditional parsimony, which is intended to avoid false-inclusion errors, is inappropriate for developing predictive models, as it leads to simplified, rigid, and closed representations of ecological systems observed under certain specific conditions. We therefore suggest a new, complementary kind of parsimony that limits assumptions on systems conditions in order to avoid false-exclusion errors. This leads to more flexible and open models that can take into account the possibility that, under different conditions, different sets of factors might dominate a system's behavior and response patterns, that is, generate a regime shift. We will use individual-based or agent-based models (ABMs) in population ecology as an example to illustrate the new parsimony we are suggesting and will finally discuss how the resulting new kind of models can foster the development of predictive ecological theory.

What Kind of Errors Should We Strive to Avoid When Constructing Predictive Population Models?

A model, by definition, is a simplified representation of a real system. The task of the modeler is to find a representation of the study system that captures the dynamics and responses of interest for the questions being asked of the model. Two basic kinds of representational errors are possible. First, the representation might identify incorrect process(es) as being essential to capture the internal organization of the system. This can lead to a type of error we here refer to as false inclusion, that is, a mechanism is included even though it is in fact not essential to the question. To avoid false inclusions, models are made as simple as possible, concentrating on major dynamics. This reduces the potential for spurious results but does so at the cost of specificity and flexibility in relation to changing conditions. Second, an alternative type of error can occur, which we refer to as false exclusion, where the model leaves out a process because it was assumed to not be essential when in fact it was. To avoid false exclusions, modelers would prefer to include rather than ignore a mechanism because under certain circumstances it might be important. This improves completeness but does so at the cost of simplicity. In the current practice of ecological model development, this type of error avoidance rarely plays a role, even in complex synthetic models for systems.

A simple example would be a population model where we might consider the details of an organism's energy budget as not being essential for explaining population dynamics and rather use age- or size-specific growth, mortality, and reproduction rates. We might know that energy budgets exist and are dynamic (Kooijman 2010; Sibly et al. 2013) and that they might also be important for population dynamics, but most modelers would prefer to avoid false inclusion, that is, they would rather accept the risk of excluding a factor that might be important than the risk of including a factor that is in fact not important. Thus, most modelers would choose simplicity as the most important design criterion. A recent study has demonstrated, however, that at least under fully closed and controlled laboratory conditions, inclusion of dynamic energy budgets was essential to develop a model that was able to predict the response of the population to new environmental conditions (Martin et al. 2013).

Another more complex example is the case of the North Atlantic cod fishery. Here, as in many other cases, an a priori oversimplification of models can be understood as an "arrogant" approach (sensu Cilliers 2005), on the basis of the assumption that we are able to identify from the outset which processes should be left out. This arrogance can lead to disaster when these models serve as the basis for managing the use of natural resources. In the case of the North Atlantic cod fishery off the coast of North America, age-structured population models failed to capture system dynamic relationships between the increasing anthropogenic catchability factors operating over time and the density-dependent catchability. These factors together led to the dramatic collapse of the Atlantic cod (*Gadus morhua*) population (Walters and Maguire 1996). These factors were not unknown. Rather, they were ignored because modeling parsimony focused on the avoidance of false inclusions. Although fishermen warned that the cod had disappeared from suboptimal habitat and that their fishing effort was concentrated in optimal habitat, continued reference to the key variable of constant catch rates, which were now associated only with stock depletion in optimal habitat, led to an incorrect assessment of the population's state (Nenadovic et al. 2012).

Avoiding false-inclusion errors helps ensure the rigor of ecological models by focusing attention on important general principles associated with central phenomena. Models based on descriptions of the central phenomenon of density-dependent growth rates usually avoid representation of specific processes. In this way, they also avoid false inclusions. However, these models have limited capabilities for taking into account situation-specific changes and have, on that basis, been considered "remarkably useless in solving management problems or in providing an understanding of why populations change in size" (Krebs 2002, p. 1211).

As a complement to the currently dominant type of parsimony, we suggest a new kind of parsimony that limits assumptions on systems conditions to avoid false-exclusion errors. This approach would also aim to take into account existing knowledge about, for example, adaptive behavior, energy budgets, variations in space and time, and trait-mediated interactions to provide a flexible, mechanistic,

and open representation of the multitude of processes from which density-dependent population growth can emerge. For example, to model the response of winter survival of shorebirds to changes in their feeding habitat and, hence, density, Goss-Custard, Stillman, and co-workers took into account tides, heterogeneous distribution of prey, energy budgets, optimal foraging, and interference competition among individuals to generate representations of novel behaviors (Stillman and Goss-Custard 2010).

In fact there are increasingly important questions concerning how populations and ecosystems develop over time in response to changing external and internal conditions that require models to include representations of novel behaviors. Since novelty is, by definition, unexpected, it cannot be meaningfully represented using minimalist models focused on false-inclusion avoidance. This is because the dynamic response pathways available to any living system are determined by more than the prevailing conditions in the external environment and the basic characteristics of the responding system; they are also determined by the types of change mechanisms (e.g., genetic change, relocation, and prey-switching) at the disposal of that system (Prigogine 1978) and by complex and ambiguous relationships between exogenous and endogenous dynamics (Schneider and Kay 1995). Consequently, what we often need to do is to understand what might occur, providing a range of possibilities and probabilities of potential outcomes. To understand emergent dynamics in these systems, modeling approaches that avoid false exclusions are required, formalizing representation not of the system's reliable simplicity but of its surprising complexity.

From Static and Closed to Flexible and Open Representations: The Role Played by Scientific Narratives

Ideally, we want to predict, with a reasonable degree of accuracy, the potential reactions, responses, and adaptations that might be seen in populations facing, for example, anthropogenic changes to climate and habitat. To do this, what is required are not snapshot models that represent the present characteristics of these populations, including how they currently respond to change, but flexible models that also represent the populations' behavioral patterns and reactivity dispositions. Such models should be systematically related to what might be expected to happen when both the population and its environment are changing simultaneously. Doing this requires a critical preliminary analysis of which drivers and mechanisms might be needed to simulate the system for a wide range of environmental conditions; variable and parameter choices must, in effect, be informed by preliminary modeling of the system, which is intended to reduce the likelihood of false exclusions. The key advantage of synthetic models is that we often can indeed model the response of their building blocks, small spatial units and individual organisms, to a wide range of conditions and then let system-level responses emerge from the responses of the building blocks and their interactions.

Where Krebs and Berteaux (2006) saw this requirement carrying with it the risk of ecologists turning into little more than storytellers, consideration of stories told about the behavior of the system and its components should play a larger role in synthetic model development. By "storytelling" we mean reports about certain sequences of events that are linked by causal relationships, for example, the observation of fisherman that cod disappeared from suboptimal habitat because they moved to better sites that were depleted of cod due to overfishing. Such stories should not be dismissed as being "anecdotal" because they can provide critical information about how a certain system functions under different conditions. Reports on causal chains of events have been referred to as "scientific narratives" (Prigogine 1997), an approach discussed in disciplines where history and contingency are important for understanding (Millington et al. 2012), such as sociology (e.g., Abell 2004), ecology (e.g., Brown 2011), and geology (e.g., Cleland 2011). Millington et al. (2012) discuss why narratives should be used more often in ecology: "the narrative approach . . . complements, rather than replaces, statistical portraits of aggregated system-level outcomes" (p. 1027).

As with the cod example, we argue that attempting to (over)simplify models to provide as concise a description of the problem as possible is counterproductive when dealing with complex systems. Oversimplification comes with an increased likelihood that even small changes in drivers and conditions will invalidate predictions of system responses, since each simplification removes a factor that may turn out to have a minor but sometimes important role in determining how the system changes in response to the changed inputs. On the other hand, all models are simplifications, and all potentially critical details of the system cannot always be included in the model.

To balance false-inclusion and false-exclusion error avoidance, we suggest adopting a "modest approach" (sensu Cilliers 2005) with respect to modeling the complexity of living systems. Simplification is still needed, to get iterative model development and refinement started (Grimm and Railsback 2005), but this can work only if the output of each iterative model version is compared with data and observed patterns (Grimm et al. 2005). Imposing fixed simplification a priori is a dangerous practice when modeling systems whose stability properties—in particular, resilience—are maintained through a complex combination of opportunities, redundancy, creativity, and positive and negative feedback loops, all operating simultaneously and across multiple spatial and temporal scales.

A posteriori simplification of traditional population models is easier to justify, in that mechanisms are dropped on the basis of some initial understanding of the modeled system's behaviors; this approach has been referred to as "robustness analysis" of computational models (Railsback and Grimm 2012). However, this approach still presumes that the modeled system resides within unchanging bounds throughout the runtime of the model. This simplification reduces the potential of the model to accurately predict system responses to (1) changes that take place within the system in the course of the processes being modeled (Holling and Meffe 1996; Anderies et al. 2006) and (2) new input parameter values not yet seen in the real world.

A pluralistic modest approach generates a well-documented array of possible scenarios of system development whose usefulness can be evaluated on the basis of a review of model presumptions, model output, and real-world situations. By adopting a modest position and fully documenting our knowledge concerning the limits of the models we build, we describe the character and extent of their "wrongness" and thereby highlight the range of their usefulness (see also Augusiak et al. 2014). Essentially, we suggest replacing static snapshots with models that allow the exploration of a wider range of scenarios. Adopting this pluralistic and dynamic approach might have helped to prevent, for example, the collapse of the North Atlantic cod fishery mentioned above. Similarly, the financial crisis of 2008 might have been anticipated with such an approach—and better coped with afterward (Silver 2012).

To achieve the right mix of avoiding false inclusions and false exclusions and to represent scientific narratives, ABMs are the most flexible approach and thus play a special role. ABMs based on a more balanced consideration of parsimony will still focus on avoiding false inclusions to represent mechanisms operating at lower hierarchical levels (e.g., individuals) and local spatial scales. Examples include energy budgets of individuals (Topping et al. 2010; Martin et al. 2013); adaptive behavior, such as optimal foraging (Stillman and Goss-Custard 2008); habitat selection (Railsback and Harvey 2013); and generic representations of interactions among individuals (Berger and Hildenbrand 2000; Weiner et al. 2001).

The initial focus on avoiding false inclusions at the level of submodels should then be complemented by avoiding false exclusions at the level of the full model. In this part of the process, we are concerned with developing a relevant representation of the complexity of the study system. Here, the conventional model development work of finding variables and processes that can be removed should be complemented by checking for important variables and processes that might have been missed as they might become relevant under new conditions.

Regarding the distinction between false inclusions and exclusions we propose here, there is to date no population model that has explicitly taken this into account. However, this note is based on the lessons learned in a number of projects where ABMs were developed within a framework that comes close to the one we suggest (Topping et al. 2010, 2013; Stillman et al. 2015).

Conclusions

Basing understanding of population dynamics mainly on models that focus on avoiding false inclusions is unreliable because both external and internal conditions change the way populations—and indeed ecosystems—develop over time. However, as stated by Beardsley (2010), "biology may have awkward properties, but it is not beyond science's power to manage them" (p. 327). To achieve greater reliability in population ecology, we advocate the incorporation of an approach that is complementary to false-inclusion avoidance: false-exclusion avoidance. ABMs play a particularly important role in this, as they can include both more traditional representation of the behavior of spatial units and individuals and system-level representations in the form of "stories" about possible causal sequences of events that might become important, depending on how the system and its environment change over time. This allows us to take into account the full range of knowledge that is available about a certain system and the general principles that might apply to it. These models, which can take into account patterns of change over time, appear to us to be a more appropriate tool for predicting population change in the complex socioecological contexts that constitute an increasingly important part of population ecology studies. It makes no sense to expect potentially surprising future states to be predictable on the basis of reference to statistical tables that represent the most stable basic features of a population's established change dynamics. The challenge here—and in predictive ecology more generally—is to engage directly with the complexity of the problem rather than factoring it away. To do this, we propose that population ecology must, for example, learn how to work productively with complex stories told by experts, which detail a variety of potential development pathways for a population.

To achieve predictive systems models, we need to integrate traditional approaches, which focus on rigorous descriptions of stable system features by avoiding false inclusions, with complementary approaches that focus on scientific narratives, which help us to avoid false exclusions.

Having more population models that make correct predictions about responses to new conditions will also foster theory development. Any submodel representing a particular behavior that leads to correct predictions is a can-

didate for a tested and valid theory of this behavior. This is different from theories in, for example, behavioral ecology because the theories are tested not in isolation but within the context of an entire ABM of a certain system ("pattern-oriented theory development"; Railsback and Grimm 2012).

Last but not least, developing models that include factors that are important under one set of conditions but not others will help in the exploration and better understanding of regime shifts and resilience (Scheffer et al. 2009). This is much harder, if not impossible, with static models that tie a representation to certain conditions but is facilitated by adding the avoidance of false exclusions as a complementary modeling approach.

Acknowledgments

We are grateful to the reviewers and editors whose efforts helped to improve this note.

Literature Cited

Abell, P. 2004. Narrative explanation: an alternative to variable-centred explanation? Annual Review of Sociology 30:287–310.

Anderies, J., B. Walker, and A. Kinzig. 2006. Fifteen weddings and a funeral: case studies and resilience-based management. Ecology and Society 11:21.

Augusiak J., P. J. van den Brink, and V. Grimm. 2014. Merging validation and evaluation of ecological models to "evaludation": a review of terminology and a practical approach. Ecological Modelling 280:117–128.

Beardsley, T. M. 2010. Disentangling complexity in biology. Bioscience 60:327.

Berger, U., and H. Hildenbrandt. 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. Ecological Modelling 132:287–302.

Brown, B. 2011. Ecology as historical science. Pages 251–282 *in* K. deLaplante, B. Brown, and K. A. Peacock, eds. Handbook of the philosophy of science. Vol. 11. Philosophy of ecology. Elsevier, Oxford.

Cilliers, P. 2005. Complexity, deconstruction and relativism. Theory, Culture, and Society 22:255–267.

Cleland, C. E. 2011. Prediction and explanation in historical natural science. British Journal for the Philosophy of Science 62:551–582.

DeAngelis, D. L., and W. M. Mooij. 2003. In praise of mechanistically-rich models. Pages 63–82 *in* C. D. Canham, J. J. Cole, and W. K. Lauenroth, eds. Models in ecosystem science. Princeton University Press, Princeton, NJ.

Goss-Custard, J. D., and R. A. Stillman. 2008. Individual-based models and the management of shorebird populations. Natural Resource Modeling 21:3–71.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecological Modelling 115:129–148.

Grimm, V., and S. F. Railsback. 2005. Individual-based modeling and ecology. Princeton Series in Theoretical and Computational Biology. Princeton University Press, Princeton, NJ.

Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H. H. Thulke, J. Weiner, T. Wiegand, and D. L. DeAngelis. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310:987–991.

Holling, C. S., and G. K. Meffe. 1996. Command and control and the pathology of natural resource management. Conservation Biology 10:328–337.

Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory: computer simulations show that many ecological patterns can be explained by interactions among individual organisms. Bioscience 38:682–691.

Kooijman, S. A. L. M. 2010. Dynamic energy budget theory for metabolic organisation. Cambridge University Press, Cambridge.

Krebs, C. J. 2002. Two complementary paradigms for analysing population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1211–1219.

Krebs, C. J., and D. Berteaux. 2006. Problems and pitfalls in relating climate variability to population dynamics. Climate Research 32: 143–149.

Martin, B. T., T. Jager, R. M. Nisbet, T. G. Preuss, and V. Grimm. 2013. Predicting population dynamics from the properties of individuals: a cross-level test of dynamic energy budget theory. American Naturalist 181:506–519.

Millington, J. D., D. O'Sullivan, and G. L. Perry. 2012. Model histories: narrative explanation in generative simulation modelling. Geoforum 43:1025–1034.

Nenadovic, M., T. Johnson, and J. Wilson. 2012. Implementing the Western Gulf of Maine Area Closure: the role and perception of fishers' ecological knowledge. Ecology and Society 17:20.

Prigogine, I. 1978. Time, structure, and fluctuations. Science 201: 777–785.

———. 1997. The end of the certainty: time, chaos, and the new laws of nature. Free Press, New York.

Railsback, S. F., and V. Grimm. 2012. Agent-based and individual-based modeling: a practical introduction. Princeton University Press, Princeton, NJ.

Railsback, S. F., and B. C. Harvey. 2013. Trait-mediated trophic interactions: is foraging theory keeping up? Trends in Ecology and Evolution 28:119–125.

Roughgarden, J., A. Bergman, S. Shafir, and C. Taylor. 1996. Adaptive computation in ecology and evolution: a guide for future research. Pages 25–32 *in* R. K. Belew and M. Mitchell, eds. Adaptive individuals in evolving populations: models and algorithms. Santa Fe Institute Studies in the Science of Complexity. Addison-Wesley, Reading, MA.

Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, et al. 2009. Early-warning signals for critical transitions. Nature 461:53–59.

Schneider, E. D., and J. J. Kay. 1995. Order from disorder: the thermodynamics of complexity in biology. Pages 161–172 *in* M. P. Murphy and A. J. O'Neill, eds. What is life? the next fifty years: speculations on the future of biology. Cambridge University Press, Cambridge.

Sibly, R. M., V. Grimm, B. T. Martin, A. S. A. Johnston, K. Kułakowska, C. J. Topping, P. Calow, J. Nabe-Nielsen, P. Thorbek, and D. L. DeAngelis. 2013. Representing the acquisition and use of energy by individuals in agent-based models of animal populations. Methods in Ecology and Evolution 4:151–161.

Silver, N. 2012. The signal and the noise: why so many predictions fail—but some don't. Penguin, New York.

Stillman, R. A., and J. D. Goss-Custard. 2010. Individual-based ecology of coastal birds. Biological Reviews 85:413–434.

Stillman, R. A., R. F. Railsback, J. Giske, U. Berger, and V. Grimm. 2015. Making predictions in a changing world: the benefits of individual-based ecology. BioScience 65:140–150.

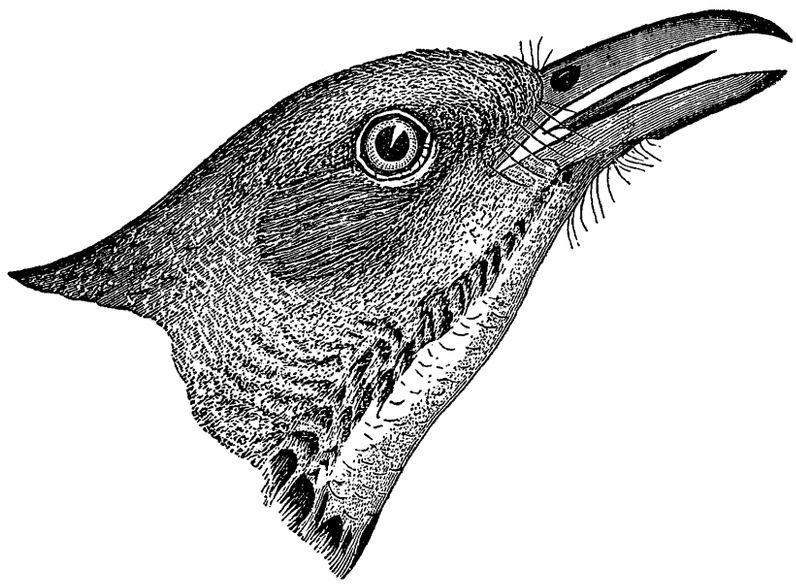
Topping, C. J., T. T. Hoye, and C. R. Olesen. 2010. Opening the black box: development, testing and documentation of a mechanistically rich agent-based model. Ecological Modelling 221:245–255.

Topping, C. J., P. Odderskær, and J. Kahlert. 2013. Modelling skylarks (*Alauda arvensis*) to predict impacts of changes in land management and policy: development and testing of an agent-based model. PLoS ONE 8:e65803.

Walters, C., and J. J. Maguire. 1996. Lessons for stock assessment from the northern cod collapse. Reviews in Fish Biology and Fisheries 6:125–137.

Weiner, J., P. Stoll, H. Muller-Landau, and A. Jasentuliyana. 2001. The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. American Naturalist 158:438–450.

Associate Editor: Uta Berger
Editor: Judith L. Bronstein



"Almost every one knows the Brown Thrush, or Thrasher (*Harporhynchus rufus*) of the Eastern United States—an abundant and familiar inhabitant of shrubbery, and a spirited songster, with some talent for mimicry. It belongs to the mocking-thrush group (*Miminæ*) all of which are famous for their vocal powers; the cat-bird, and the princely mocking-bird itself, are near relatives. The accompanying cut . . . looks something like a thrasher in the act of singing." From "Some United States Birds, New to Science, and Other Things Ornithological" by Elliott Coues (*The American Naturalist*, 1873, 7:321–331).