The Journal of Wildlife Management; DOI: 10.1002/jwmg.21568

Letter to the Editor

Testing *A Priori* Hypotheses Improves the Reliability of Wildlife Research

MICHAEL S. MITCHELL,[1] *U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, 205 Natural Sciences Building, University of Montana, Missoula, MT 59812, USA*

SARAH N. SELLS, *Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, 205 Natural Sciences Building, University of Montana, Missoula, MT 59812, USA*

KRISTIN J. BARKER, *Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, 205 Natural Sciences Building, University of Montana, Missoula, MT 59812, USA*

SARAH B. BASSING, *School of Environmental and Forest Sciences, 107 Anderson Hall, University of Washington, Seattle, WA 98125, USA*

ALLISON C. KEEVER, *Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, 205 Natural Sciences Building, University of Montana, Missoula, MT 59812, USA*

SHANNON C. FORSHEE, *Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, 205 Natural Sciences Building, University of Montana, Missoula, MT 59812, USA*

JAMES W. GOERZ, *Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, 205 Natural Sciences Building, University of Montana, Missoula, MT 59812, USA*

We appreciate the contributions of Gula and Theuerkauf (2018) to what we hope will be an ongoing discussion within the wildlife profession. Their response to Sells et al. (2018) reflects a common perspective in wildlife biology (Romesburg 1981, Williams 1997) that our synthesis of the history, logic, and practice behind the concept of rigorous science was intended to address. Although the arguments put forth by Gula and Theuerkauf (2018) are useful and thought-provoking, they suggest a misunderstanding of key points made by Sells et al. (2018) regarding the logical strengths of hypothesis testing, the relative merits of *a posteriori* hypotheses, and why *a priori* hypotheses are useful for wildlife management.

THE LOGIC OF HYPOTHESIS TESTING

Sells et al. (2018) presented nothing novel about the contribution of hypothesis testing to scientific rigor, drawing instead on the thinking of eminent scientists and philosophers over the centuries of scientific practice (Crombie 1962, Platt 1964, Romesburg 1981, Losee 1993, Gauch 2003). As Sells et al. (2018) noted, scientific methodology has deep roots dating to Ancient Greece and has been "basically correct and complete" for >700 years (Gauch 2003:163). Key to this methodology is the idea that science uses logic to draw inferences about reality from empirical observations, but not all forms of logic are equally rigorous (Romesburg 1981, Losee 1993, Williams 1997, Gauch 2003). Testing *a priori* hypotheses draws on the syllogistic logic of *modus tollens* (i.e., positing predictions from a hypothesis, comparing predictions to observations, refuting the hypothesis if predictions do not accord with observations), which holds that inferences based on falsification of a hypothesis are more strongly supported than those based on *post hoc* interpretation of observations (Williams 1997, Copi and Cohen 2005, Sells et al. 2018). This logic applies to any research intended to yield inferences about processes that produce what is observed (Platt 1964, Romesburg 1981, Hilborn and Mangel 1997, Williams 1997, Sells et al. 2018). Gula and Theuerkauf (2018) do not provide a logical alternative to *modus tollens* to support their contention that studies of "properties of local populations. . .[do] not fit the H-D scheme" and that "presence of an *a priori* hypothesis is not of importance" for observational (i.e., descriptive) studies.

Gula and Theuerkauf (2018) also describe a debatable dichotomy between hard and soft science, suggesting that hypothesis testing only applies to the former. They assert that the fields of evolutionary biology, genetic coding, cell biology, physiology, and some ecology can have characteristics of hard science, whereas wildlife biology is complex (incorrectly implying the other fields are not), and thus a soft science. The application of rigorous science is not limited solely to simple, easily reduced systems. Scientists by definition reduce complexity of any system they study using models, developed either inductively or deductively (Sells et al. 2018:488). Such models cannot reproduce every detail of the system being studied; instead they presume that simplified representations can produce predictions generally consistent with complex reality (Levin 1992). Nothing about complexity of a system therefore precludes rigorous science. On the contrary, a rigorous scientific approach contributes strongly to understanding complex systems by requiring explicit, *a priori* justification for models based on mechanistic influences with the greatest potential importance (e.g., using

Received: 12 August 2018; Accepted: 13 August 2018

[1]*E-mail: mike.mitchell@umontana.edu*

biological arguments to justify the choice of land cover types used in a resource selection function; Boyce and McDonald 1999).

Gula and Theuerkauf (2018) argue that hypotheses must be of "universal character" and "proven and established as theory" to provide reliable predictions, and that "universal laws" are not appropriate for management decisions. These assertions suggest a misunderstanding of hypotheses and how they inform research and management. Hypotheses amend theory (i.e., the body of existing knowledge); they do not constitute it and they are not by definition universal (Williams 1997, Sells et al. 2018:491). Rather, they are preconceived notions about how existing theory might be credibly adapted to explain observations in a studied system (e.g., properties of a local wildlife population). Tests of well-defined hypotheses thus have implications specific to the system being studied and more generally for the body of existing knowledge.

For most, if not all species of management interest, existing natural history, ecological theory, and prior research are sufficient to posit at least some *a priori* hypotheses for ecological processes that are explanatory for any population. Gula and Theuerkauf (2018) assert that a study designed to determine sustainable harvest quotas for a local population necessitates "a long-term study that is basically descriptive." On the contrary, explicitly stating and testing *a priori* hypotheses based on the broad body of knowledge available to wildlife researchers offers the greatest potential for understanding dynamics of a harvested population (and thereby maximizing scientific contribution to management objectives). For example, researchers studying a harvested population of black bears (*Ursus americanus*) might test hypotheses about the relative importance of adult survival and juvenile recruitment for population growth (Gaillard et al. 1998, Raithel et al. 2007, Mitchell et al. 2009), the relative effects of food resources and social interactions on population density (Young and Ruff 1982, Beckmann and Berger 2003, Mitchell and Powell 2007), or whether harvest mortality is additive or compensatory (Obbard and Howe 2008). Results of these hypothesis tests would allow managers to set more informed harvest quotas for the population while efficiently directing limited resources to monitor demographic and environmental factors most strongly associated with its response to harvest. Given the ample fodder for developing *a priori* hypotheses, it is difficult to argue that the logical strength of rigorous science should be voluntarily sacrificed to conduct observational studies if they add little to what can be readily derived from existing natural history, research, and theory. Additionally, there is no more effective way to demonstrate important idiosyncrasies of a population than falsifying a hypothesis shown to be predictive for other populations.

THE IMPORTANCE OF UNTESTED HYPOTHESES

We agree with Gula and Theuerkauf (2018) that observational and exploratory studies can make contributions to wildlife science. If the goal of research is simply to estimate statistical parameters, *a priori* hypotheses are unnecessary (although such estimates are often used to draw biological inferences that would benefit from hypothesis testing). Observational studies can be useful when lack of existing natural history, research, or theory hinders development of *a priori* hypotheses (a rare circumstance in modern wildlife research; Mitchell et al. 2018). Observational and exploratory studies can also offer important *a posteriori* explanations for observed patterns, providing the foundation for *a priori* hypotheses that subsequent studies can test (Sells et al. 2018:492). Not all *a posteriori* explanations are equally useful, however. An observational study that produces *post hoc* inferences that add little to existing knowledge is of limited utility. By contrast, a study that tests *a priori* hypotheses drawn from existing knowledge can proffer *a posteriori* hypotheses that explicitly show how future research can contribute novel insights. Importantly, a falsified *a priori* hypothesis creates the opportunity for the substitution of an improved *a posteriori* hypothesis.

THE UTILITY OF HYPOTHESIS TESTING TO MANAGEMENT

Wildlife managers seek to manipulate complex ecological systems to achieve objectives. An important role of applied research is to identify which among many biological processes most strongly contribute to a desired outcome and how they might be managed to achieve it. Such insights are most useful to managers when they are reliable and timely. Reliability implies correct understanding of the biological processes contributing to a desired outcome (Romesburg 1981) so that management efforts will not be wasted on manipulating the wrong processes or incorrectly manipulating the right processes. Timeliness implies that research results are available to managers on temporal scales relevant to the decisions they must make; few managers have the luxury to wait for the results of long-term studies or a critical mass of short-term studies to inform their decisions. Reliability and timeliness of research results, therefore, imply the need for efficiency. Depending on the accumulation of *post hoc* inferences from observational studies to correctly understand biological processes is inherently inefficient, requiring considerable time, money, and effort before patterns are revealed through repetition or meta-analysis. By contrast, rigorous science can be highly efficient because it relies on a 2-fold process of elimination: formulating *a priori* hypotheses by narrowing the breadth of available research precedents, theories, and ideas to a subset directly relevant to a specific management challenge, and decisively discarding those hypotheses that do not prove explanatory or useful for achieving management objectives. A small number of rigorous studies, therefore, can provide reliable information needed by managers in a short period of time compared to what a large number of observational studies might eventually provide.

Generality of research results can play an important role in management decisions because managers often draw on what studies have shown for other, similar populations. This approach benefits from an understanding of the degree to which results of one study may be applicable elsewhere. Observational research describes a pattern specific to a place and time and may speculate about general mechanisms. By contrast, rigorous research can explicitly test for general mechanisms that might underlie observed patterns, depending on the research questions being asked (Sells et al. 2018:488–489). This approach has the potential to clearly distinguish idiosyncratic processes observed in a single population (e.g., effects of a local harvest strategy on a population of white-tailed deer [*Odocoileus virginanus*]) from general mechanisms (e.g., factors that influence vital rates for hunted populations of white-tailed deer) that may be influential for other populations. Thus, testing *a priori* hypotheses can produce more generally applicable information than observational studies, allowing managers to make better-informed decisions for times and places outside the scopes of individual studies.

Finally, hypothesis testing is implicit in most wildlife management because decisions are based on notions of how a system works and how it can be manipulated to achieve a goal. The ability to regularly achieve goals suggests uncertainty associated with these notions may not be an impediment to understanding and managing the system. When goals are not regularly achieved, however, alternative notions may need to be considered to reduce uncertainty and thereby improve management efficacy. Rigorous research that tests hypotheses reduces uncertainty efficiently compared to the slow accumulation of observational research or to eventual meta-analyses. The growing field of adaptive management makes this advantage an explicit part of making management decisions, whereby hypotheses about system processes and how they are affected by management actions are posited *a priori*, then tested through subsequent monitoring (Lancia et al. 1996, Nichols and Williams 2006, Williams et al. 2007); the reliable inferences produced efficiently reduce the uncertainty impeding effective management decisions. Adaptive management is thus logically consistent with and best informed by rigorous science.

THE BOTTOM LINE OF HYPOTHESIS TESTING

The strength of scientific inferences can vary considerably among different approaches of conducting scientific inquiry. Arguably, research informing wildlife conservation calls for strong scientific rigor because consequences of misinformed management can be substantial (Romesburg 1981, Williams 1997, Sells et al. 2018). Because science is inherently question-driven, it is reasonable to posit compelling answers to the questions *a priori* and determine which are supported by data. Deriving those answers can draw on abundant empirical and theoretical precedent and new ideas that challenge reigning paradigms. Discarding unsupported answers reduces uncertainty where *post hoc* inferences cannot (Sells et al. 2018:492), resulting in research that is efficient in reliability, timeliness, and expenditure of human and financial capital. We know of no better logical means to rule out uninformative, dated, or irrelevant biological concepts and to identify opportunities for developing improved alternatives that better serve management needs. Similarly, we know of no more efficient way to reliably evaluate efficacy of management practices. Except for the rare circumstances where research seeks to understand truly novel systems and how they might be managed, we argue that the logic, practicality, and efficiency of hypothesis testing offers substantially greater benefit to wildlife conservation than purely observational studies.

ACKNOWLEDGMENTS

We thank R. Gula and J. Theuerkauf for contributing to what we hope will be an ongoing discussion within the wildlife profession. We also thank A. D. Luis and L. S. Mills for their valuable feedback on previous versions of this manuscript.

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