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Review

Confronting Uncertainty: Contributions of the Wildlife Profession to the Broader Scientific Community

JAMES D. NICHOLS,[1] *U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708, USA*

ABSTRACT Most wildlife professionals are engaged in 1 or both of 2 basic endeavors: science and management. These endeavors are a focus of many other disciplines, leading to widespread sharing of general methodologies. Wildlife professionals have appropriately borrowed and assimilated many methods developed primarily in other disciplines but have also led the development of one class of quantitative methods, those that confront and incorporate uncertainty. Uncertainty arises in counts of focal entities, for which wildlife professionals have developed effective methods to deal with the common problems of nondetection and misclassification. These methods have been borrowed by disciplines as varied as paleobiology, medicine, human epidemiology, industrial quality control, military target acquisition, remote sensing, and human census. Uncertainty also arises in the modeling of those counts, specifically the observation and ecological processes that generated them. Wildlife professionals recognized the fundamental importance of model selection and rapidly assimilated methods for selecting the most appropriate model for a given data set. These methods for dealing with uncertainty inherent to counting and modeling are critical to the conduct of science and management. Wildlife professionals have developed additional methods for incorporating uncertainty in the accumulation of knowledge and the development of optimal decisions in an environment of learning. In some cases, professionals in other disciplines are using methods developed and popularized in the wildlife profession, but there is much potential for greater use. In this essay, I describe these areas of wildlife leadership, document their assimilation by other disciplines, and emphasize the potential for more interdisciplinary use of these methods.

KEY WORDS counts, interdisciplinary, management, models, quantitative methods, science, uncertainty, wildlife profession.

Members of the wildlife profession engage in 2 basic endeavors: science and management. Because of their fundamental nature, these 2 endeavors are a primary focus of other disciplines also, leading to basic methodological approaches that are shared by many fields. As a result, many quantitative methods used by wildlife biologists derive, or directly borrow, from methods developed in other disciplines. For example, many key ideas in hypothesis testing and experimental design now used in virtually all scientific disciplines were developed in agricultural research (Fisher 1947, 1958). Methods for drawing inferences about an entire population based on sampling are widely used in wildlife research and management and were developed in such varied fields as human survey sampling and quality control for manufacturing (Cochran 1977, Thompson 2002). Models for projecting wildlife population dynamics were borrowed directly from human demographers (Lotka 1907, 1956; Keyfitz 1968).

This appropriation by the wildlife profession of methods developed by the greater scientific community is sensible, as it would be foolish to waste effort reinventing methods that already exist. In fact, we expect the methods used in any scientific discipline to represent a mix of some approaches developed within the discipline and others borrowed from the larger scientific community. Given the age and relative funding levels associated with the wildlife profession, we might expect relatively small contributions to methods useful in other disciplines. Although humans have long harvested wildlife populations, wildlife biology as a science is young, in North America tracing back to Aldo Leopold's (1933) *Game Management*. Many other scientific disciplines have existed for centuries, developing methods over these longer time horizons. Methodological development also depends on research funding, with some disciplines, for example, those closely associated with human health and national defense, receiving much more funding than wildlife, and hence devoting much more effort to methodological research.

In this essay, I focus on methodological approaches to which the wildlife profession has made substantial contributions, particularly quantitative methods that confront or

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[1]*E-mail: jamesdnichols2@gmail.com*

deal with uncertainty. Whereas other disciplines recognize uncertainty, they frequently ignore some forms of uncertainty or assume that they are of little consequence to science and management. In contrast, wildlife professionals have confronted uncertainty and dealt with it directly, making contributions that are disproportionate to those expected based on the discipline's age and funding levels. I argue that the importance of these contributions has not been fully realized, as there are numerous disciplines that stand to gain from incorporation of these approaches into their methodological toolboxes. I begin by describing uncertainty associated with 2 endeavors common to most disciplines: counting and modeling. I review contributions by wildlife professionals to confronting uncertainty in these 2 endeavors, and then turn to their larger roles in science and management.

UNCERTAINTY IN COUNTING

Data collection frequently entails counting entities of interest, and errors in counting can bias parameter estimates based on counts. Wildlife professionals use counts to infer such quantities as the number of animals in a population or their annual survival rate. Two main sources of uncertainty typically characterize use of counts to estimate parameters. The first source stems from the inability to count animals in a focal population at every location where they occur. For example, we frequently attempt to estimate animal abundance over spatial expanses so large as to preclude counts over the entire area. In such cases, we try to select a sample of locations where we conduct counts in a manner that permits inferences about locations where we do not count. Most disciplines recognize this source of uncertainty, leading to development of probabilistic sampling methods (e.g., simple random sampling, stratified random sampling; Thompson 2002), which are appropriately used by wildlife professionals. Wildlife applications have motivated development of some sampling methods (e.g., adaptive cluster sampling; Thompson 1990), but the profession has not otherwise contributed substantially to this methodological development. The second source of count uncertainty emerges during the counting process itself, which is often characterized by non-negligible probabilities of nondetection and misclassification. At the locations where we do conduct counts, we typically do not detect all entities, and we misclassify some of those that we do detect. The wildlife profession has been a leader in addressing the 2 components (nondetection and misclassification) of this latter source of uncertainty in the counting process itself.

Nondetection

Whenever we count wild animals to estimate abundance, survival, or recruitment, we nearly always miss some individuals. In the simplest case, the number of animals that we detect and count (C_{it} for site i and time t) is treated as a binomial random variable with expectation given by the product of true abundance (N_{it}) and detection probability (p_{it}; the probability that an animal present in the surveyed area is detected and counted):

$$E(C_{it}) = N_{it} p_{it} \tag{1}$$

The count is known, so if detection probability can be somehow estimated, then abundance can also be estimated:

$$\widehat{N}_{it} = \frac{C_{it}}{\widehat{p}_{it}} \tag{2}$$

where the hats denote estimators (Lancia et al. 1994). The key to use of Equation (2) is the ability to estimate the detection probability associated with the count, and wildlife professionals have devoted substantial thought and effort to this problem.

Wildlife biology.—Frederick Lincoln was a federal biologist who banded birds and used recoveries of these bands reported by the public to study migration patterns. He also developed a way to use banded ducks and their recoveries to estimate the abundance of the North American duck population. Lincoln (1930) developed his estimator intuitively, using marked ducks recovered by hunters to estimate the probability that a duck would be harvested (detection probability) and then dividing an estimate of the total harvest (the count) by this probability to estimate waterfowl abundance just prior to the hunting season (the time of banding). Lincoln's estimator is noteworthy for 1) combining data of 2 different types (banding and recovery data, and hunter survey data) within a single estimation framework, an approach used increasingly by wildlife scientists to reduce uncertainty in estimated quantities (Pollock 1982, Burnham 1993, Besbeas et al. 2002, White and Lubow 2002, Gopalaswamy et al. 2012, Osnas et al. 2016); and 2) acknowledging that not all ducks were banded, and that the banded total needed to be corrected for nondetection to estimate abundance. Previously, Petersen (1896) had used similar thinking to estimate size of a fish population based on marked animals and their recaptures (LeCren 1965). Lincoln's (1930) estimator inspired an enormous amount of effort to develop models for estimating abundance, survival, and other population parameters from capture-recapture studies in which animals are caught, marked, released back into their populations and then recaptured via subsequent sampling (Otis et al. 1978, Seber 1982, Pollock et al. 1990, Lebreton et al. 1992, Amstrup et al. 2005).

Other approaches for estimating animal abundance based on imperfect counts were developed also, including distance sampling (Burnham et al. 1980, Buckland et al. 2001), double-observer models (Cook and Jacobson 1979, Nichols et al. 2000), time at detection methods (Farnsworth et al. 2002), and N-mixture models (Royle 2004, Kéry and Royle 2016). Occupancy can be viewed as the fraction of some region, or the proportion of spatial sample units within the region, that is occupied by a focal species. Just as individuals are missed in counts for animal abundance, species surveys do not always detect species that are present. Species detection data from repeated surveys conducted on spatial sample units over time or space can be used with capture-recapture thinking and Equation (2) to estimate occupancy. As with capture-recapture, distance sampling, and some of the other approaches for abundance estimation, occupancy modeling has been the subject of major effort by biologists and biostatisticians over the past 15 years, with many models now available (Bailey et al. 2014, MacKenzie et al. 2018). Despite the different focal parameters of interest and the different field sampling approaches on which these various methods are based, they all reflect the recognition of the importance of detection probability to inference, using the conceptual framework provided by Equation (2). Many disciplines share this uncertainty associated with incomplete counts. Most disciplines faced with undercounts and incomplete detection recognize the issue, but many have either not thought it a problem warranting research effort or dealt with it via *ad hoc* approaches, rather than the more formal statistical inference methods used by wildlife scientists. In some cases, the disciplines have appropriated methods developed by wildlife professionals, but in other cases wildlife methods have been recommended but not widely adopted. The discussion below thus focuses on the methodological contributions of the wildlife profession to other disciplines (Table 1), recognizing that many of these contributions have not been fully realized. The disciplines of animal population ecology and community ecology are so closely related to wildlife ecology that I make no substantive distinction here. Indeed, animal ecologists have contributed substantially to the methodological development that I attribute to the wildlife profession.

Paleobiology.—There is a clear analogy between field sampling methods for wildlife populations and fossil taxa. The paleobiologist samples strata of material representing different periods of geologic time, counting taxa that can be identified from each period or stratum. However, taxa that were extant in the focal period or stratum are invariably missed, leading to undercounts of taxa actually present. Nondetection is recognized by paleobiologists (Foote and Raup 1996), and detection probabilities are thought to vary across time and space (Brett 1998). Animal ecologists and wildlife biologists have clearly demonstrated the direct applicability of various capture-recapture and occupancy modeling approaches to inference in paleobiology (Rosenzweig and Duek 1979, Rosenzweig and Taylor 1980, Nichols and Pollock 1983, Nichols et al. 1986, Liow and Nichols 2010), and these methods have seen limited use (Connolly and Miller 2001*a*, 2001*b*, 2002; Liow 2013). I expect these methods to eventually become standard in paleobiology, leading to changes in our understanding of temporal and spatial variation in taxonomic diversity and associated rates of extinction and origination (Conroy and Nichols 1984, Nichols et al. 1986).

Social sciences.—Governments of most countries include agencies charged with periodic censuses of human populations. Regardless of counting methods, human censuses virtually always represent undercounts. Laplace (1786) derived an estimator (the same one later developed independently by Lincoln [1930] and Petersen [1896]) for the human population of France based on 2 lists of citizens and their degree of overlap. Sekar and Deming (1949) again appeared to derive the Lincoln estimator independently to draw inferences about the numbers of human births and deaths in a district near Calcutta, India. More recently, scientists working with the United States Census Bureau have borrowed and sometimes extended capture-recapture models to estimate the census undercount (Wolter 1986, 1990; Cowan and Malec 1986). Social scientists have borrowed capture-recapture models to make inferences about hidden populations, such as the number of homeless people in a city (Cowan et al. 1986) and demographic parameters of criminal populations (Greene 1983). I recently worked with social scientists to use reports from different news agencies to estimate the number and geographic distribution of incidents of political unrest. Even though humans are sometimes easier

Table 1. Multidisciplinary uses of wildlife inference methods that deal with nondetection.

Discipline	Inference targets	Wildlife methods	Representative citations
Paleobiology	Taxonomic diversity and rates of extinction, origination	Capture–recapture and band recovery models	Rosenzweig and Duek (1979), Nichols and Pollock (1983)
	Taxonomic spatial distribution	Occupancy models	Liow (2013)
Social sciences	Human census	Capture–recapture models	Laplace (1786)[a], Sekar and Deming (1949)[a], Wolter (1986)
	Number of homeless	Capture–recapture models	Cowan et al. (1986)
	Demography of criminals	Capture–recapture models	Greene (1983)
	Incidents of political unrest	Capture–recapture models	J. D. Nichols (U.S. Geological Survey, unpublished data)
Human epidemiology	Within-population disease dynamics	Capture–recapture models	Wittes and Sidel (1968), Hook and Regal (1995), Jennelle et al. (2007)[b]
	Between-population spatial disease dynamics	Dynamic multistate occupancy models	Adams et al. (2010)[b], McClintock et al. (2010*b*)[b]
Literature	Author vocabulary size	Capture–recapture models	Efron and Thisted (1976)
Software development	Number of errors	Capture–recapture models	Chao and Yang (1993)
Manuscript proofing	Number of errors	Capture–recapture models	White et al. (1982)
Philately	Number of existing rare stamps	Capture–recapture models	Herendeen and White (2013)
Space exploration	Number of orbiting manmade objects	Capture–recapture models	K. H. Pollock (North Carolina State University, personal communication)

[a] Estimators of Laplace (1786) and probably Sekar and Deming (1949) were derived independently of wildlife methods.
[b] Cited examples focus on wildlife diseases, but methods are equally applicable for humans.

to count than wild animals, the issue of nondetection is still pervasive, and there are many exciting opportunities to apply wildlife inference methods to a wide variety of count-based problems in the social sciences. I agree wholeheartedly with the following statement by LaPorte (1994:5): "Human population science has society as its laboratory and 'counting humans' as its basis. Counting techniques, however, have changed little this century. The use of capture-recapture techniques could bring about a paradigm shift in how counting is done in all the disciplines that assess human populations."

Human health and epidemiology.—These disciplines have borrowed heavily from the wildlife profession, making use of methods for drawing inferences about abundances and rate parameters (Wittes and Sidel 1968, McCarty et al. 1993, Hook and Regal 1995, International Working Group for Disease Monitoring and Forecasting 1995, Chao et al. 2001). Many epidemiological applications of quantitative methods from wildlife focus on estimation of the number of persons contracting a specific disease in a specified time and region. The raw data are lists of persons with the disease as ascertained from such sources as hospital discharge records, prescriptions specific to the disease, reports from physician visits, and records of local government health departments, among others. The lists associated with these sources are analogous to the capture occasions in wildlife applications, and the detection histories (on which lists did each person appear) are used to estimate the number of cases appearing on no list, and hence the total number of cases.

Although this contribution of the wildlife profession to epidemiology is substantive and demonstrable, this use of capture-recapture models does not appear to be as widely accepted as it could be. A published letter to the editor of Lancet (LaPorte et al. 1992:494) began as follows:

> SIR,—Why is it that we know more about the number of sandhill cranes, monarch butterflies, sperm whales, and bison, than we know about the number of new heart attacks, cancers, injuries, and asthma attacks? It is because population biologists are better able to "count" animals than we are able to "count" diseases. Perhaps it is time to start counting non-communicable diseases (NCD) in much the same manner as wildlife biologists count sandhill cranes.

LaPorte et al. (1992:495) later commented, "It is surprising that the capture-mark-recapture methods have not made greater inroads in medicine . . ."

It is possible that the situation has changed over the last 25 years, but I see little evidence that this is the case. At a 2011 workshop that I attended on the detection and reporting of rare events, a biostatistician working for the Centers for Disease Control and Prevention outlined her approach to inference about detection probability for a focal disease. She stated that her strategy was to develop a model for each of 10–12 sources of variation in detection, with the hope that the resulting set of models could be used eventually to predict overall detection probability (J. D. Nichols, U.S. Geological Survey, personal observation). At the time of the workshop, she had developed 2 of these models and indicated that this was a long-term project. The more direct, robust, and immediately accessible capture-recapture approach would use some form of repeated sampling (e.g., multiple lists) to directly estimate detection probability and the focal parameter (e.g., number of cases of the disease). If covariates are hypothesized to influence detection probability (the sources of variation for which the statistician was developing models), then these could be used as covariates for modeling detection probability.

The point of this anecdote is simply that the assimilation of inferential methods that deal formally with detection is not complete in the epidemiological and biomedical professions, even for estimating numbers of persons experiencing certain diseases or other health problems. There appears to be even less use of open capture-recapture models that permit inference about the rate parameters that govern disease dynamics. For example, the classical compartmental (e.g., SIR) models for epidemiology of infectious diseases (Kermack and McKendrick 1927, Bailey 1975, Anderson and May 1991, Cooch et al. 2012) categorize members of a population into states (e.g., susceptible [S], infected [I], and recovered or removed [R] depending on the disease). Multiple list data at any point in time permit estimation of the number of individuals in each state, allowing for detection probabilities that likely differ among states. Multiple lists obtained at multiple points through time (e.g., every yr, every 5 yrs) can be used with multistate capture–recapture models (Arnason 1973, Brownie et al. 1993, Schwarz et al. 1993, Nichols and Kendall 1995, Lebreton et al. 2009) to permit direct inference about state-specific mortality rates and state transition probabilities (key parameters underlying disease dynamics), in the presence of state-specific detection probabilities.

Although the focus of most compartmental models is on disease dynamics within a population, spatio-temporal dynamics of epidemics at larger scales are of substantial interest also (Grenfell et al. 2001). Occupancy models permit inference about spatial distribution of disease at a single time (Adams et al. 2010) and disease dynamics through time (McClintock et al. 2010*b*, Bailey et al. 2014, Nichols et al. 2017, MacKenzie et al. 2018). Detection probabilities are clearly important to such inferences and are likely to vary across space as functions of proximity to hospitals and local physicians. In summary, I conclude that methods developed by wildlife professionals have contributed substantially to epidemiological studies and have great potential to contribute much more.

Other disciplines.—Wildlife methods have also been used to deal with nondetection in literary research (Shakespeare's vocabulary; Efron and Thisted 1976), quality control (e.g., estimation of errors in computer programs [Chao and Yang 1993] and edited manuscripts [White et al. 1982]), national defense issues (estimation of number of hidden missile silos or weapons storage facilities in hostile countries), philately (estimation of numbers of existing rare stamps; Herendeen and White 2013), and space exploration (estimation of manmade objects orbiting earth; K. H. Pollock, North Carolina State University, personal communication).

Nondetection summary.—The problem of nondetection is pervasive in count statistics of many different kinds. Wildlife professionals recognized this source of uncertainty in counts and devoted substantive effort to inference methods that permit estimation of detection probabilities and, more importantly, the focal parameters that are otherwise confounded with detection probabilities. The assimilation of these contributions has been variable across the many disciplines that use counts affected by nondetection. This variation has resulted primarily from differences among disciplines in recognizing the problem of nondetection and, conditional on recognition, appreciating the analogy with wildlife problems and assimilating the appropriate methods. Substantial benefits to many disciplines are possible with additional appropriation of methods from the diverse toolbox developed by wildlife professionals to deal with nondetection.

Misclassification

Nondetection is a special case of the more general issue of misclassification. For example, nondetection of a focal species present in a sample unit may lead to the conclusion that the unit is not occupied by the species, and this can be viewed as misclassification (labeling an area as unoccupied when it is really occupied). In the wildlife profession, however, the set of methods developed to deal specifically with nondetection is much larger and has a longer history than methods that deal more generally with misclassification, motivating the separate treatment here. I thus define misclassification as the assignment of counted entities to the wrong class or state.

Just as detection probability is the key parameter incorporating nondetection, classification probability is the more general parameter dealing with misclassification. I define classification probability, p_{ijt}, as:

$$p_{ijt} = \Pr(\text{record class } i)|(\text{true class} = j)$$

where t denotes time or sampling occasion. The analytic approaches developed to deal with misclassification (see below) include in their likelihoods p_{ij} matrices that reflect the probabilities of the various possible observation states i conditional on true state j.

Wildlife biology.—In studies of individual animals, such as those using capture-recapture data, multistate models (Arnason 1973, Hestbeck et al. 1991, Brownie et al. 1993, Schwarz et al. 1993, Lebreton et al. 2009) rely on the ability to classify detected animals using either their locations or observable state variables such as age, reproductive condition, and disease state. These models were developed assuming no uncertainty in state assignment. Multistate models accommodating state uncertainty were developed by Kendall et al. (2003, 2004), Nichols et al. (2004), and Runge et al. (2007) and generalized by Pradel (2005). Pradel's (2005) multi-event modeling approach permits inference about state-specific survival and transition probabilities in the presence of state misclassification. Investigators have begun to integrate species misclassification into double-observer and distance sampling frameworks (Conn et al. 2013).

Occupancy models (MacKenzie et al. 2002, 2018) seek to characterize spatial sample units as either occupied by a focal species or not, thus forming the basis for studies of species distribution and range dynamics. Early occupancy modeling focused only on the counting error nondetection. More recently, attention has been directed to so-called false positives, in which an investigator misclassifies an animal, or records a species as being present when it is not. Several models have been developed to estimate occupancy in the presence of false positives and false negatives (Royle and Link 2006; Miller et al. 2011, 2013; Chambert et al. 2015, 2018).

A key feature of these wildlife approaches to dealing with misclassification is that they estimate the magnitude and direction of misclassification and provide approximately unbiased estimates of focal parameters (abundance, occupancy, state-specific survival, state transition probabilities) despite misclassification. These approaches incorporate misclassification directly into model likelihoods such that this form of uncertainty is dealt with explicitly. Thus, variance estimates for focal parameters properly incorporate the additional variance component associated with this extra uncertainty.

Epidemiology.—Many laboratory assays for specific diseases admit the possibility of both false negatives (nondetection) and false positives (misclassification), leading to errors in epidemiological inferences both within populations (compartmental models) and between populations (spatial epidemiology). Studies of wildlife disease processes have used multistate capture–recapture models with state uncertainty to estimate parameters of compartmental models (Jennelle et al. 2007, Conn and Cooch 2009, Kendall 2009, Cooch et al. 2012). Kendall (2009), and McClintock et al. (2010*b*) outlined designs for use of false positive occupancy models to investigate spatial epidemiology of wildlife diseases. These wildlife applications provide roadmaps for use of similar methods with laboratory diagnostic test data for human disease problems.

Epidemiologists have recently begun to use data from the internet (e.g., classifying disease state based on symptom lists provided to diagnostic medical web sites; Woolhouse et al. 2015). Such lists can be used to draw inferences about the disease state of each subject, but misclassification is very likely. The inferential goal should not be to drive misclassification errors to 0 (an impossible task) but rather to properly incorporate such errors into the estimation of state variables and vital rates. Occupancy models with state uncertainty should be extremely useful in efforts to estimate spatial distribution and dynamics of disease from such internet data.

Remote sensing.—Aerial photography and later satellite imaging have been used to draw inferences about patterns and dynamics of land use for over half a century. Practitioners have realized that assessments of land use state (e.g., urban, agriculture, forest) based solely on images are not always correct (Veran et al. 2012). The practice of ground-truthing entails direct ground-level assessments of state and leads to classification matrices developed for the subset of sample units classified both remotely and directly. Users of remote sensing have primarily employed such data to develop classification matrices and make statements about the accuracy of their classifications. Often the correct classification probabilities (p_{ii}) are > 0.85, leading users to conclude that their results are fairly accurate. For some uses, however, this level of accuracy is not good at all. Frequently, we are interested in land use dynamics, focusing on state transition probabilities estimated from land use assessments at 2 points in time. Errors in either time period produce errors in the estimated transition, leading to levels of accuracy that are less than those for estimates (e.g., amount of land in state s) at one point in time. Veran et al. (2012) used a multistate capture-recapture modeling approach with state uncertainty to provide estimates of land use transition probabilities in the face of misclassification. I would expect this sort of approach to be adopted and widely used for inference from remotely sensed land use data.

Other disciplines.—In paleobiology, bone, shell, and other fossil fragments are sometimes misclassified and assigned to the wrong taxon. Multistate capture-recapture models including state uncertainty and dynamic occupancy models allowing for false positives will be useful for addressing questions about taxonomic diversity and extinction in the face of misclassification. Military instrumentation is often focused on target acquisition, entailing the classification of images as belonging to objects in various size classes that are either hostile or benign. An example is the performance of a periscope imaging system as a function of size and range of target objects. Methods borrowed from the wildlife discipline for modeling both detection and classification probabilities have proven useful in this specific example (Nichols et al. 2013*a*, *b*).

Misclassification summary.—Practitioners in these example disciplines are not ignorant of misclassification, and sometimes estimate classification probabilities. However, the usual approach in other disciplines is to acknowledge misclassification errors but view them as a second-order problem. Specifically, other disciplines have failed to directly incorporate classification probabilities into inference methods for state-specific abundances and state transition probabilities. Failure to deal with even small misclassification probabilities can produce substantial bias in estimates of focal parameters (Kendall et al. 2003, McClintock et al. 2010*a*, Veran et al. 2012, Miller et al. 2015). The alternative approach adopted by the wildlife community has been to develop inference methods that directly incorporate classification probabilities to provide unbiased estimates of focal parameters. Many disciplines could benefit from the state uncertainty modeling that has been developed in the wildlife profession.

UNCERTAINTY IN MODELING

Model Selection

The approach of wildlife professionals to dealing with the problems of nondetection and misclassification has been to develop analytic models that include parameters reflecting these kinds of errors: detection probabilities and classification probabilities. In the terminology of hierarchical modeling (Royle and Dorazio 2008), these probabilities are used to develop models of the observation process, the process by which count data arise from our survey methods. Some models (e.g., capture-recapture models for closed [meaning no gains or losses during the survey] populations, double-observer models, time-of-detection models, many distance sampling models) include only the observation process and are directed at estimation of focal state variables (e.g., abundance, density, occupancy) at a single point in time.

Other models (e.g., capture-recapture models for open [gains and losses between sampling occasions] populations, occupancy models) include components for both the observation process and the state process, the latter terms reflecting the temporal or spatial (or both) dynamics of the focal state variable. Most dynamic state models are represented as stochastic processes, introducing an additional form of uncertainty (e.g., demographic stochasticity for population models). Regardless of whether a modeling effort includes only the observation process or both the observation and state processes, there are virtually always multiple potential ways to characterize or parameterize any process, and thus multiple potential models. Modeling uncertainty refers to the usual multiplicity of plausible models and leads to a need to select the most appropriate model(s) from a set of candidates.

For example, assume a small study in which a species of wild ungulate is surveyed using dependent double-observer sampling along line transects (Cook and Jacobson 1979) deployed in 2 sites characterized by different land cover types, wet forest with dense understory and dry forest with sparse understory. The study objective focuses on the state process and is to compare ungulate densities in the 2 land cover types (denote as D_W and D_D). The observation process component of the modeling must consider the possibility that overall (both observers combined) visual detection probabilities (p_W, p_D) may also differ between the 2 types. For this simple situation, the most complex model would include both detection parameters and both density parameters, indicating different detection probabilities and ungulate densities in the 2 land cover types. The simplest model would include just a single detection parameter ($p_. = p_W = p_D$) and a single density parameter ($D_. = D_W = D_D$), and the other 2 possibilities would be only density and only detection differing between land cover types. The resulting 4 models might be denoted as (D_L, p_L, where L denotes land cover type), (D_L, $p_.$), ($D_.$, p_L), and ($D_.$, $p_.$). Model selection seeks to reduce the uncertainty associated with these possible models by selecting the most appropriate model(s), given the available data. This reduction in uncertainty is important whether our focus is on estimation (e.g., density estimates are required for management of the 2 sites) or understanding (e.g., does density differ between the 2 sites according to an *a priori* hypothesis about the superiority of dry forest). Model selection with this latter focus on state process is a key step in the conduct of science (see below).

Wildlife Biology

The history of interest in selection among candidate models in the wildlife profession is decades old. Brownie et al. (1978) considered a small set of models for estimating survival rates from waterfowl band recovery data. Their models were nested, in the sense that every model could be obtained by placing constraints on the parameters of the most general model. Brownie et al. (1978) thus recommended sequential likelihood ratio testing for model selection (also see Burnham et al. 1987, Pollock et al. 1990). Otis et al. (1978) developed multiple capture-recapture models to estimate abundance for closed animal populations. These models were not nested, so Otis et al. (1978) simulated data under the different models, computed goodness-of-fit and between-model test statistics, and then used these statistics to develop a discriminant function for model selection. Burnham and Anderson (1992) and Lebreton et al. (1992) introduced the wildlife and animal ecology disciplines to Akaike's Information Criterion (AIC) as a viable approach to parsimonious model selection that did not depend on nested models. This approach and its small sample and quasilikelihood variants have become widely used (Burnham and Anderson 2002). The Bayesian Information Criterion and Bayes factors have been recommended to the wildlife community (Link and Barker 2006, 2009), as has Reversible jump Markov chain Monte Carlo (Brooks et al. 2002, Barker and Link 2013). A powerful approach to model selection is based on out-of-sample validation, with other viable approaches including the Deviance Information Criterion and Watanabe's Information Criterion (Hooton and Hobbs 2015).

Other Disciplines

With a few exceptions (Otis et al. 1978, Barker and Link 2013), the discussed approaches to model selection were not actually developed by wildlife researchers. However, the wildlife discipline was among the first to recognize the fundamental importance of model selection to the scientific enterprise and to popularize and advocate its use as a necessary step in all inference. This led to rapid assimilation of a model selection philosophy in wildlife science and has spread to most scientific disciplines, with model selection now an important component of many scientific papers. The influence of wildlife scientists on this popularization of model selection is illustrated by the important book on this topic by Burnham and Anderson (1998, 2002), which has been cited >43,000 times (Google Scholar, Nov 2018) by investigators in many disciplines.

UNCERTAINTY IN SCIENCE

The wildlife profession has thus provided substantial leadership in the development of quantitative methods to deal with uncertainty in counting and modeling. However, these methods are not inherently useful in isolation but rather attain utility when properly used in the endeavors of science and management. Wildlife professionals have developed approaches to dealing with these sources of uncertainty in the conduct of these broader endeavors.

Science

Science is a process developed to reduce uncertainty and is the most successful approach that humans have devised to do so. The initial step in the scientific process is the development of hypotheses to explain how the world, or typically a part of it, works. These hypotheses may originate in almost any manner, typically via human use of inductive or deductive mental processes. The objective of the overall scientific process is to determine which hypothesis in a set of reasonable candidates seems to provide the best description and predictions for the focal natural process. To do this, models are constructed for each hypothesis to develop testable predictions. Observations are then made of the studied process, which may (but need not) be manipulated to facilitate discrimination among models and thus hypotheses. The key step in science is then comparison of observations against model-based predictions, with consistency between the 2 taken as evidence that the model (and its hypothesis) is a viable and plausible explanation of the underlying natural process.

Counting attains value to science in providing the observations used in the scientific process. Modeling is used to estimate relevant variables and parameters from the counts and to provide predictions. Comparison of estimates and model-based predictions is sometimes conducted using a 2-step process. First, count-based estimates of state variables and associated vital rates are obtained, using described methods for dealing with count uncertainty. Second, these estimates are compared with model-based predictions to assess their consistency. This procedure is followed for ≥ 2 models, and the model providing predictions most consistent with observations gains support. The other, more modern, approach to this comparison is to develop multiple models that incorporate both observation and state processes, to fit these models to the single set of observations, and to then use a model selection approach to determine which hypothesis or hypotheses show the greatest consistency with observations. Both approaches must deal with counting uncertainty and include a final step of model selection to reduce modeling uncertainty in the state process.

Accumulation of Knowledge

This brief description of the conduct of science is applicable to a single set of observations, regardless of whether they arise via experimentation or monitoring. Science, however, is not a one and done process, as all uncertainty is seldom eliminated by a single comparison of observations and predictions. Instead, science is best viewed as a progressive and cumulative endeavor (Descartes 1637), with hypotheses that predict well gaining more and more support with each comparison of predictions and new observations. In most disciplines, this accumulation of knowledge occurs, at best, in an *ad hoc* manner. Single investigators (or groups) conducting long-term studies sometimes obtain provisional answers to one question before moving on to subsequent hypotheses, thus tracking within-study accumulation of knowledge.

Introduction and Discussion sections of scientific papers frequently review the evidence for and against a focal hypothesis based on past studies. However, few papers provide a formal assessment of the degree to which knowledge was advanced by their results.

Meta-analyses represent attempts to assess accumulated knowledge at specific points in time. Meta-analyses were adapted from other disciplines by ecologists and wildlife scientists in the early 1990s. The term meta-analysis has been used in multiple ways, with one meaning corresponding to "the statistical analysis of a large collection of analysis results from individual studies for the purpose of integrating the findings" (Glass 1976:3). Frequently, meta-analyses are conducted using results from multiple published papers focusing on a specific question (Gurevitz et al. 2001, Korichava et al. 2013). Summary statistics in selected papers are subjected to secondary analysis intended to provide an overall inference. Such meta-analyses do not represent a systematic approach to reduction of uncertainty but provide assessments of accumulated knowledge at specific points in time.

Other meta-analyses, such as those undertaken by wildlife professionals for population dynamics of spotted owls (*Strix occidentalis* spp.) in the western United States (Franklin et al. 2004, Dugger et al. 2016), entail periodic modeling of long-term data sets from multiple study locations. Each successive analysis is based on a longer time series of data because new data are added since the previous analysis. These meta-analyses were originally focused on estimation of trend statistics, rather than on mechanistic hypotheses, but the planned periodic nature of these meta-analyses is consistent with the idea of progression and accumulation of knowledge.

A more formal approach to progressive reduction in uncertainty (knowledge accumulation) is based on Bayes' theorem and has been advocated by fisheries and wildlife sciences since the mid-1970s (Walters and Hilborn 1976, Walters 1986, Johnson et al. 1993, Williams 1996*a*, Hilborn and Mangel 1997). We can define the information state of a scientific process as a vector of model weights, π_t (model i), for model i at time t, that reflect the relative predictive abilities of models in the model set. If there are M models in the set, then:

$$\sum_{i=1}^{M} \pi_t(\text{model } i) = 1$$

Because these model weights reflect relative predictive abilities, we have more confidence in the models with higher weights and view them as more likely to represent reasonable abstractions of the focal natural processes. Model weights prior to the first set of observations can be based on historical information, intuition, or simply set equal ($1/M$) for each model. However, subsequent model weights potentially change with each new set of observations, evolving according to:

$$(\pi_{t+1}(\text{model } i)|\text{data}_{t+1}) = \frac{\pi_t(\text{model } i)\Pr(\text{data}_{t+1}|\text{model } i)}{\sum_i^M \pi_t(\text{model } i)\Pr(\text{data}_{t+1}|\text{model } i)} \qquad (3)$$

where Pr(data $_{t+1}$ |model i) is the probability that the new (time $t+1$) observations would have arisen, given that model i was a good representation of the actual process that generated them. This approach, Equation (3), specifies that the updating of model weights is based on the relative confidence in the model that has accumulated through time t, π_t (model i), and the consistency of the new set of observations with that model, Pr(data $_{t+1}$ |model i). Note that computation of Pr(data $_{t+1}$ |model i) must consider uncertainty associated with both counting and predictions from a stochastic state process model, and that the expression, Equation (3), provides a basis for model selection.

There are multiple advantages of this formal updating approach for accumulation of knowledge, when compared with stand-alone studies or even meta-analyses. For example, recent work on model selection methods favors out-of-sample predictions as a good approach (Hooten and Hobbs 2015), and each time step's Pr(data $_{t+1}$ | model i) entails exactly such a predictive comparison. The recent evidence of the lack of reproducibility of many published scientific studies (Ioannidis 2005, Begley and Ioannidis 2015) should provide a major impetus for this systematic approach of repeated confrontations of predictions and observations.

This use of an evolving information state to characterize scientific learning is rare but has seen some use in the wildlife profession, always (to my knowledge) in association with a management program (Johnson 2011, Nichols et al. 2015, U.S. Fish and Wildlife Service 2018). I have not seen this approach used in other disciplines. Much of the statistical research on inference methods focuses on single studies, and most research papers are treated as stand-alone studies, despite perfunctory allusions to other work in Introduction and Discussion sections. Similarly, most statistical research on design of experiments and surveys is based on the prospect of a single study and associated analysis. In a program of inquiry focused on the accumulation of knowledge based on multiple experiments or sets of observations, the information state is an important determinant of the optimal experimental manipulation or set of observations to conduct (W. L Kendall, Colorado State University, and J. D. Nichols, unpublished data). Programs of inquiry entailing sequences of studies offer important opportunities to speed the rate of learning, to provide results that are reproducible, and to resolve questions that multiple isolated studies do not seem able to answer effectively. My hope is that wildlife professionals will show even more leadership by promoting this logical approach to learning, to the point where programs of inquiry eventually become common in all disciplines, as has been the case for single-study model selection.

UNCERTAINTY IN MANAGEMENT AND DECISION-MAKING

Management

Wildlife management is a profession that focuses on making decisions and taking selected actions designed to change natural systems in a manner consistent with specified objectives. The task of the decision-maker at each decision point is to select the action that is best, where best is defined with respect to specified objectives. In the absence of uncertainty about current system state and system response to potential actions, this selection is a straightforward optimization problem (Williams et al. 2002). However, system state (e.g., population size) is seldom known but instead is estimated from monitoring data with both counting and modeling uncertainty. Similarly, we require models to predict system response to management actions, and must thus confront modeling uncertainty and uncertainty associated with stochastic system dynamics.

The basic approach to making an informed decision is similar for processes that are and are not characterized by uncertainty. At each decision point, the decision is made based on program objectives, available actions, the model projecting system responses to actions, and the state of the system as estimated from the monitoring program. An important distinction between decision processes that are and are not characterized by these sources of uncertainty is in the decision algorithms used to compute optimal solutions (see below).

Modeling uncertainty about system response requires more than a specific kind of decision algorithm. Fisheries and wildlife scientists (Walters and Hilborn 1976, 1978; Walters 1986; Johnson et al. 1993; Williams et al. 2007) developed a process labeled adaptive resource management (ARM) that inserts a scientific step into the decision process. Instead of basing predicted system response to actions on a single model, multiple models are used. Conditional on the state of the system at time t and the selected action, predictions are made by each model about system state at time t+1. State is estimated by the monitoring program and compared against each of the model-based predictions, with model weights, π_t (model i), increasing for models that predict well and decreasing for those predicting poorly. So knowledge accumulates as for a scientific process, and the relative weights of the evolving information state play an important role in selecting the best action.

Optimization with Uncertainty

Decision algorithms for selecting the best management action are quantitative methods that can be tailored to specific sources of uncertainty. Many decisions are state-specific. In single-species population management, we might take very different actions if the population is much smaller versus much larger than our population goal. At any decision point, the manager selects an action based on objectives, available management actions, model-based predictions about system response to each action, and current state of the system (e.g., population size in the example). Because system state changes as a result of both natural processes and management actions, an optimal decision at decision point t must account for the predicted system state at time t+1 and other variables associated with objectives. If the objective is to maximize wildlife harvest over a long time horizon, for example, an optimal decision at time t must be one that not only produces immediate harvest (usually) but also leaves a population size that can support harvests in year t+1 and the future. Optimization in such a dynamic problem must thus consider predicted system dynamics in future time steps and deal with attendant uncertainty.

Uncertain state dynamics.—Stochastic dynamic programming (SDP) was developed in the 1950s (Bellman 1957) to solve dynamic optimization problems characterized by stochasticity. Stochastic dynamic programming deals explicitly with the uncertainty of predicted state dynamics and has been widely adopted by the variety of disciplines requiring decisions for managing such processes. Development of SDP is based on first-order Markov decision processes, for which system state at time t+1 is a function of system state at time t, management actions taken between t and t+1, and environmental conditions occurring between t and t+1. Although it is not as widely used in the wildlife profession as it should be, SDP has been used to make wildlife decisions for some time (Anderson 1975; Williams 1982, 1989; Lubow 1995). Wildlife professionals played no major role in the development of optimization methods for dealing with the uncertainty associated with dynamic stochastic processes, but they have used these methodological developments as appropriate.

Standard SDP does not deal adequately with the 2 sources of uncertainty identified above in association with counting and modeling. Stochastic dynamic programming assumes that system state at the time (t) of the current decision is known, whereas in the wildlife profession system state is virtually always estimated. Estimates have accompanying variances that reflect uncertainty associated with both spatial sampling (counts are not obtained on the entire area of interest) and counting (counts are incomplete and characterized by misclassification). In addition, SDP assumes a single dynamic model and was not designed to account for multiple plausible models of system dynamics. Stochastic dynamic programming has been extended to deal with these additional sources of uncertainty, and these extensions have seen use in the wildlife profession.

Counting uncertainty.—Partially observable Markov decision processes (POMDP) are dynamic decision processes for which system state is not known, for example because of counting uncertainty (Astrom 1965, Smallwood and Sondik 1973, Monahan 1982). Dynamics within POMDP focus on a belief state, a probability distribution of values of true state. For discrete state variables such as animal population size, the belief state consists of a probability mass for each possible value of true state. Belief state at time t+1 is a function of the belief state at t, the action taken between t and t+1, and the count-based estimate of system state at t+1. Belief states thus evolve through time as estimates accumulate, with the optimization at each time step accounting for this source of uncertainty. Partially observable Markov decision processes are beginning to see use in a few disciplines, and wildlife managers are becoming an important user group (Chadès et al. 2008, Williams 2011, Fackler and Pacifici 2014).

Modeling uncertainty.—Decision-making requires a model of system response to available management actions, but frequently we consider multiple plausible models of response.

The dynamic optimization extension developed to deal with model uncertainty has been labeled adaptive stochastic dynamic programming (ASDP; Williams 1996*a*, *b*; Lubow 1997; Williams et al. 2002). Adaptive stochastic dynamic programming incorporates the dynamics of the focal state variables (e.g., population size) and those of the information state, defined above as the vector of model weights, π_t (model i), reflecting relative confidence in the models of the model set. In SDP, optimization is based on the projected responses of the managed system to each of the potential actions and entails selection of the action that yields the response most consistent with program objectives. In the case of multiple models, ASDP uses a weighted average of projected responses from the different models, where the weights are the elements of the information state. Models with greater weights thus exert greater influence in determination of the optimal decision. The information state evolves with new data according to Equation (3), and knowledge accumulates. Adaptive optimization is focused on both current returns and reduction in modeling uncertainty; better decisions and returns are expected as model uncertainty is reduced. Wildlife scientists are among the leaders in developing and implementing ASDP, with relatively little use by other disciplines.

Multiple sources of uncertainty.—Recent work in the wildlife profession on dynamic optimization has provided approaches to deal simultaneously with both counting and modeling uncertainty, and the uncertainty of the modeled stochastic process, by following the current and projected joint distribution of belief state (counting uncertainty) and information state (modeling uncertainty; Williams 2009, 2011; Fackler and Pacifici 2014). This approach should see increasing use in the future as software is developed to facilitate its implementation. Recent developments also clarify how to use information collected outside of the management process itself. Initial approaches to adaptive management (Walters and Hilborn 1976, 1978; Walters 1986; Johnson et al. 1993; Williams et al. 2007) and optimization (ASDP; Williams 1996*a*, *b*; Lubow 1997) based changes in model weights at each decision point on the correspondence of predicted and estimated system state, where the latter came from monitoring associated with the management program. However, research external to the management program is frequently designed to provide information useful in discriminating among competing models. The conceptual framework has been developed to use information internal and external to the management program to resolve modeling uncertainty (Williams 2015).

Optimization with uncertainty: summary.—Decision algorithms (e.g., optimization) used in wildlife management and many other disciplines must deal with the sources of uncertainty that characterize the overall decision process. Three main sources of uncertainty are those associated with the stochastic processes governing system dynamics (source 1), the inability to know (and the resultant need to estimate) system state (source 2), and the existence of multiple plausible models of system dynamics (source 3). Many disciplines, including wildlife, have recognized source 1 and use SDP to obtain optimal solutions for dynamic systems. Several disciplines, wildlife among them, have recognized sources 1 and 2 and made initial efforts to deal with them, for example using POMDP. Few disciplines have recognized both sources 1 and 3, and the wildlife profession has been among the leaders in efforts to deal with modeling uncertainty. Similarly, very few disciplines have recognized all 3 sources and made efforts to deal with them simultaneously, and the wildlife profession is becoming a leader here as well.

Managing with Uncertainty

Wildlife profession.—Dealing formally with modeling uncertainty requires a decision algorithm that can incorporate multiple models and a process designed to reduce this uncertainty. Wildlife and fisheries professionals have been leaders in recognizing modeling uncertainty about how systems respond to management actions (Leopold 1933, Beverton and Holt 1957, Anderson 1975, Walters and Hilborn 1976) and developed ARM in response to this recognition (Walters and Hilborn 1976, 1978; Walters 1986; Johnson et al. 1993; Williams et al. 2007). The ARM approach has been adopted by a number of wildlife management programs (e.g., Johnson et al. 1993, Martin et al. 2011, McGowan et al. 2015, Williams et al. 2007, U.S. Fish and Wildlife Service 2017) but is not as widely used as could be hoped (Nichols 2017).

Other disciplines.—Many other professions could benefit from the use of formal approaches to dealing with uncertainty when making informed decisions. For example, structural health monitoring seeks periodic assessments of the structural integrity of buildings, bridges, ships, airplanes, and other structures (Nichols and Murphy 2016). Decisions about when damage requires repair and how to operate mobile structures that may be accumulating damage (e.g., decisions about ship speed conditional on sea state [calm vs. rough] and on damage state of the ship hull) can certainly benefit from methods of dynamic optimization that incorporate uncertainty (Nichols et al. 2014, Nichols and Murphy 2016). Many military and business decisions are made in environments characterized by modeling uncertainty. The United States Army recently identified operational adaptability as a capstone concept for operating under conditions of uncertainty (U.S. Army Training and Doctrine Command 2009), emphasizing the need to learn and adapt to evolving enemy strategies.

Public health decisions are made in the face of all 3 sources of uncertainty listed above. As a result, ARM approaches to disease control and intervention strategies have been recommended (Bogich et al. 2013, Shea et al. 2014) but have seen little use in human epidemiology to my knowledge. The ARM process used to set annual hunting regulations for North American mallard ducks (*Anas platyrhynchos*; U.S. Fish and Wildlife Service 2017) can be characterized as scientific, defensible, transparent, and objective. We have every right to expect these same characteristics of processes for making annual decisions about influenza vaccination strategies in the United States.

SUMMARY AND CONCLUSIONS

The principal endeavors of wildlife biologists, science and management, require use of a variety of quantitative methods. The wildlife profession has borrowed many quantitative methods from other scientific disciplines but has assumed a leadership role in developing methods that incorporate and confront uncertainty. Counting focal entities is common to many disciplines, and important sources of uncertainty in counting are nondetection and misclassification. A key contribution of wildlife scientists was to develop models for the observation processes that give rise to these errors and to incorporate these models directly into models of state processes. These methods are beginning to be used in other disciplines, and many opportunities for additional uses remain. Another source of methodological uncertainty in many disciplines is the usual multiplicity of plausible models of how observations arise and, more importantly, how systems behave and respond to management actions. Wildlife scientists were among the first to recognize the central importance of model selection and to promote its use as an essential step in virtually any investigation.

This development and use of quantitative methods for dealing with uncertainty are important to the conduct of larger endeavors, science and management. The key step of science is the comparison of observations with predictions of competing models of system state processes. For a single set of observations, model selection provides a basis for estimating key parameters and discriminating among state process hypotheses. Some wildlife professionals have begun to formally accumulate knowledge via the evolution of an information state, elements of which are periodically updated using comparisons of model-based predictions and new observations. This systematic approach to reducing uncertainty has the potential to increase both reproducibility and rates of learning and should become more widely adopted in wildlife and other disciplines.

Dynamic optimization is required for deriving optimal solutions to recurrent decision problems in many disciplines. Sources of uncertainty in such optimization include the stochastic processes that describe system dynamics, the observation processes that give rise to counts, and the multiplicity of plausible models of system response to management actions. The wildlife discipline has been one of a few groups focused on optimization methods for dealing with all these sources. Wildlife professionals have been leaders in developing ARM programs to manage wisely in the present, while simultaneously accumulating knowledge (reducing modeling uncertainty) to make better decisions in the future, and such programs should see greater use in wildlife and other disciplines.

Why is it that wildlife professionals have focused on methods for dealing with uncertainty, whereas scientists from many other disciplines have not? I do not know the answer but hypothesize potential contributing factors. First, the magnitude of uncertainty is greater in wildlife investigations than in many studies of other disciplines. Counting errors in disciplines such as physics, engineering, manufacturing, and even agriculture (bushels of yield) are often relatively small, with high probabilities of detection and correct classification. In contrast, nondetection is pervasive in wildlife investigations, with detection probabilities often <0.5. Small magnitude of counting errors is not necessarily a good reason for ignoring them, and the consequences of even small levels of counting uncertainty can be important (McClintock et al. 2010*a*, Veran et al. 2012). Modeling uncertainty is smaller in some disciplines because many hypotheses are deduced from established theory (e.g., physics), and model selection is based on large sample sizes (e.g., time series of 45,000 observations; Nichols et al. 2003). The youth of the wildlife profession and the complexity of natural systems contribute to the relative paucity of established theory, and sample sizes are frequently small (e.g., a time series of 40 annual abundance estimates is fairly good; Zhao et al. 2017).

Second, wildlife science and management are framed by a decision context, sometimes resulting in contentious debate and corresponding scrutiny. For example, decisions about setting annual hunting regulations (Johnson et al. 1993) or timber harvest quotas (Dugger et al. 2016) depend on hypotheses about effects of these actions on focal wildlife species. Financial and political issues can polarize stakeholders into groups that predictably favor small-effect versus large-effect hypotheses, motivating the need to deal with this modeling uncertainty in a defensible, transparent, and objective manner. In contrast, theoretical ecologists may align themselves with one hypothesis or another, but investigations seldom receive such serious scrutiny by stakeholder groups or result in legal action.

Regardless of the underlying reasons, the wildlife profession has been a leader in recognizing uncertainty and confronting it. This leadership role is impressive for a young and poorly funded discipline. Nevertheless, we can do much better in assimilating methods for accumulating knowledge from multiple studies and for making wise decisions in the face of uncertainty. In addition, members of our profession can be more attentive to potential applications in other disciplines and provide help and guidance in transferring and adapting methods for other uses. Confronting uncertainty will continue to be an important task and is expected to increase in importance in the foreseeable future, as global change from a variety of sources becomes more rapid and relevant to natural systems.

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