



Understanding and Predicting Ecological Dynamics: Are Major surprises Inevitable?

Author(s): Daniel F. Doak, James A. Estes, Benjamin S. Halpern, Ute Jacob, David R. Lindberg, James Lovvorn, Daniel H. Monson, M. Timothy Tinker, Terrie M. Williams, J. Timothy Wootton, Ian Carroll, Mark Emmerson, Fiorenza Micheli and Mark Novak

Reviewed work(s):

Source: *Ecology*, Vol. 89, No. 4 (Apr., 2008), pp. 952-961

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/27651634>

Accessed: 03/07/2012 00:42

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Ecology, 89(4), 2008, pp. 952–961
© 2008 by the Ecological Society of America

UNDERSTANDING AND PREDICTING ECOLOGICAL DYNAMICS: ARE MAJOR SURPRISES INEVITABLE?

DANIEL F. DOAK,^{1,11} JAMES A. ESTES,² BENJAMIN S. HALPERN,³ UTE JACOB,⁴ DAVID R. LINDBERG,⁵ JAMES LOVVORN,¹
DANIEL H. MONSON,⁶ M. TIMOTHY TINKER,⁷ TERRIE M. WILLIAMS,⁷ J. TIMOTHY WOOTTON,⁸ IAN CARROLL,⁹
MARK EMMERSON,⁴ FIORENZA MICHELLI,¹⁰ AND MARK NOVAK⁸

¹*Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA*

²*USGS, Biological Resources Division, University of California, Santa Cruz, California 95060 USA*

³*National Center for Ecological Analysis and Synthesis, 735 State St., Santa Barbara, California 93101 USA*

⁴*Environmental Research Institute, University College Cork, Lee Road, Cork, Ireland*

⁵*Integrative Biology, University of California, Berkeley, California 94720 USA*

⁶*Biological Science Office, USGS Alaska Science Center, 1011 E. Tudor Road, Anchorage, Alaska 99503 USA*

⁷*Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064 USA*

⁸*Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637 USA*

⁹*Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA*

¹⁰*Hopkins Marine Station, Stanford University, Pacific Grove, California 93950 USA*

Abstract. Ecological surprises, substantial and unanticipated changes in the abundance of one or more species that result from previously unsuspected processes, are a common outcome of both experiments and observations in community and population ecology. Here, we give examples of such surprises along with the results of a survey of well-established field ecologists, most of whom have encountered one or more surprises over the course of their careers. Truly surprising results are common enough to require their consideration in any reasonable effort to characterize nature and manage natural resources. We classify surprises as dynamic-, pattern-, or intervention-based, and we speculate on the common processes that cause ecological systems to so often surprise us. A long-standing and still growing concern in the ecological literature is how best to make predictions of future population and community dynamics. Although most work on this subject involves statistical aspects of data analysis and modeling, the frequency and nature of ecological surprises imply that uncertainty cannot be easily tamed through improved analytical procedures, and that prudent management of both exploited and conserved communities will require precautionary and adaptive management approaches.

Key words: *adaptive management; ecological dynamics; food webs; prediction; stochasticity; surprises; uncertainty.*

INTRODUCTION

Surprising, or at least unanticipated, outcomes are the norm in many areas of science. If we did not routinely face surprising results, we would have little reason to continue formulating, rejecting, and recasting our views of nature. Therefore, it is not surprising, so to speak, that we frequently face outcomes of experiments and observations that leave us scratching our heads, wondering how we could have been so wrong in our expectations. Still, while a lack of perfect predictive power is to be expected, it is not so obvious why

ecologists and conservation biologists frequently face results that directly contradict their general expectations. Although such results provide fertile ground for further scientific research, they are less welcome in the context of resource management, where being at least approximately correct in our predictions is the most basic premise upon which decisions are made.

Over the last decade, there has been increasing recognition that ecological predictions must be advanced with clear statements of their uncertainty. How best to choose the model or models for predicting population and community dynamics, and how best to then define and present the uncertainties in these predictions, have been active and contentious topics in statistical and ecological research (e.g., Hilborn and

Manuscript received 18 June 2007; revised 6 August 2007;
accepted 14 August 2007. Corresponding Editor: A. M. Ellison.

¹¹ E-mail: ddoak@uwyo.edu

Mangel 1997, Burnham and Anderson 2002, Johnson and Omland 2004). Here we are not so much interested in the nuances of these analytical approaches to uncertainty as in their generally implicit assumption that the suite of formal or informal models being considered for predictive use includes some reasonable characterization of the relevant and important ecological processes, thus providing qualitatively accurate predictions. We contend that this assumption is not well-founded in experience: that the extent and frequency of major “surprises” in ecological systems argue for substantial humility about our predictive abilities, and that current effort to enumerate uncertainties must be better tempered with the recognition that ecological models fail to capture many instances of population and community dynamics.

To make this argument, and to offer an explanation for the frequent failure of ecological predictions, we begin by discussing the ways in which predictions most frequently and spectacularly fail, providing some examples to illustrate different types of surprises. Next, while acknowledging that the diverse causes of these failures make such a classification difficult, we present our view of why many of these failures occur. We then review the main emphases in the ecological literature concerning predictive uncertainty, and explain why these methods are inadequate to deal with the scope and magnitude of ecological surprises. We end with a discussion of how best to acknowledge and incorporate surprises into management practice. Although we are interested in all ecological phenomena, our focus here is largely on the dynamics of populations and communities and on surprises involving biological reactions and interactions, rather than ecosystem-level shifts or climate changes that are themselves unpredictable (for discussions and examples of ecosystem-level surprises, see Scheffer et al. 1993, 2001, Carpenter 2003, Frost et al. 2006, Genkai-Kato 2007).

SURPRISES ARE COMMON AND EXTREME

Before delving into why ecological predictions fail, we must make the case that the occasional observation of truly surprising results is the norm in ecology, not the exception. To do so, we provide a series of examples that illustrate the range of ecological surprises and present results from a survey of experienced research ecologists. We adopt the following definition of an ecological surprise: a substantial change in the abundance of one or more species resulting from a previously unknown or unanticipated process of any kind (i.e., behavior, demography, species interactions, physical forcing, and so on). Beyond this admittedly vague definition, we suggest that although many surprises may start with a seemingly minor observation, true “surprises” often have broad implications, extending geographically, taxonomically, or across multiple ecological systems. Even more importantly, real surprises almost always occur in the presence of clear knowledge and apparent

understanding, rather than due to simple ignorance. That is, an ecological surprise occurs when an experienced biologist with clear, well-informed expectations faces outcomes or patterns that strongly contradict these expectations.

To structure our presentation of examples, we classify surprises into three general types: (1) “dynamic surprises,” changing population numbers or community compositions that were directly observed and that were unanticipated or even diametrically opposed to expectations from past observations, experiments, or theories; (2) “pattern-based surprises,” spatial patterns in population abundance and community structure or data on past, often long-term, patterns of change that are dramatically inconsistent with widely accepted formal or informal models of how nature works; and (3) “intervention-based surprises,” unexpected dynamics arising from management actions or other large, human perturbations. We offer these categories not as crisp and fundamentally distinct types, but as a useful breakdown for discussion. Dynamic and pattern-based surprises differ most clearly in whether surprising results are observed as they occur vs. being seen in a spatial pattern or a record of temporal changes that have already happened. Intervention surprises are really a subset of dynamic surprises, but they provide some of the most spectacular examples, in large part because management interventions can push ecological dynamics farther and faster than do most naturally occurring processes.

Dynamic surprises

Multiple examples of ecological surprises come from time series of population numbers. Young (1994) reviewed several dozen studies to emphasize that a common expectation of ecologists and wildlife biologists—relatively stable numbers of medium and large-bodied mammals through time—was manifestly false. Wolda (1978) showed that populations of insects in the tropics are just as variable as populations of temperate species, again contradicting a large body of theory that predicted the opposite. Both these cases are striking because the expectations they contradicted were firmly entrenched and widely believed (Egerton 1973). Notably, these and similar examples of population-level surprises result in part from misperceptions about species interactions. In the case of mammalian populations, disease and predation are often assumed to be weak regulating forces, whereas for tropical insects, competition and natural enemies (as well as relatively invariant abiotic environments) have been assumed to regulate populations to low and constant densities.

Other dynamic-based surprises involve the direct observation of community interactions. Examples of such surprises range from those that are obvious in hindsight to the still inexplicable. The extremely rapid increase and spread of spruce bark beetle in south-central Alaska and the Yukon Territory during the 1990s killed over 1.19 million ha of mature white spruce trees in

Alaska alone (Matsuoka et al. 2006). The onset, speed, and extent of this outbreak were not anticipated because the previously known risk factors for bark beetle outbreaks (in particular, stand age structure) did not fully explain these widespread and sustained infestations (Berg et al. 2006). Substantial warming during this time period is now believed to be responsible for the beetle increases, but obtaining clear support for this explanation took many years of study (Berg et al. 2006).

Two examples from marine ecosystems in Alaska illustrate less understood surprises, both involving unanticipated arrivals of unexpected community members. In 1992 large numbers of smooth lumpfishes (*Aptocyclus ventriosus*) suddenly and unexpectedly appeared in coastal waters of the central and western Aleutian archipelago. These fish were so abundant that wind-rows of their dead bodies formed on the beaches. This influx, among other effects on nearshore communities, dramatically reduced nutrient limitation of sea otters, which fed extensively on the newly arrived lumpfishes (Watt et al. 2000). After this influx, sea otters had significantly improved body condition (Monson et al. 2000) and the normally large number of beach-cast carcasses of otters dying from starvation (Laidre et al. 2006) disappeared entirely. Lumpfishes had become much less common by 1993 and had disappeared almost entirely by 1994. Although Kenyon (1969) reported a similar phenomenon in the mid 1960s, the researchers involved had never seen smooth lumpfishes nor any evidence of their existence in 22 previous years of fieldwork in the Aleutian Islands, and have not seen them in the last 14 years. The reason for this unexpected "resource pulse" (sensu Ostfeld and Keesing 2000) is still entirely unknown.

Studies of sea otters and kelp forests in southwest Alaska provide a second example of an ecological surprise. In the early 1990s, killer whale sightings by researchers working on sea otters and kelp forests in the Western Aleutian archipelago rose from less than one sighting per year to multiple sightings per day. A substantial decline in sea otter numbers was evident by the mid-1990s (Doroff et al. 2003) and by the late 1990s it had become apparent that this reduction was most likely due to increased killer whale predation (Estes et al. 1998). Although the sea otter population collapse predictably led to a collapse in the kelp forest ecosystem (Estes et al. 1998, 2004, Reisewitz et al. 2006), the proximate cause of this change, arrival of a new top predator and a novel feeding behavior, was entirely unanticipated and its ultimate cause remains both uncertain and highly contentious (for a parallel case, see Roemer et al. [2002]).

Experimental studies of granivory in Chihuahuan desert scrub ecosystems by Brown and Heske (1990) provide similarly surprising results. These studies were initially designed and undertaken to understand competitive interactions among granivorous rodents, birds, and ants. One of the experimental treatments involved the removal of a guild of three kangaroo rat species

(*Dipodomys* spp.). Fortuitously, Brown and Heske continued to maintain and monitor the experiments for years after the planned experiment had ended. More than a decade later, the manipulated areas switched from desert scrub to grassland. This change, apparently due to reduced seed predation by kangaroo rats on the large-seeded grasses and reduced physical disturbances by the kangaroo rats that made seed caches more easily accessible to other granivores, was entirely unanticipated and the reason for the time lag is still unknown.

Pattern-based surprises

Pattern-based are perhaps the hardest group of surprises to recognize because we often concoct ad hoc explanations for any static pattern we observe and usually have little information with which to test our explanations. Nonetheless, observations of past changes in community composition or of the current spatial arrangement of populations and communities are sometimes very surprising, given widely-held expectations. The richest source of pattern-based surprises is paleoecological studies. The classic work of Davis (1969) on changing forest assemblages during the Holocene is one such example, as this work challenged views of community succession and, even more fundamentally, of the factors shaping consistent community structure. More recent paleontological studies are similarly surprising, showing that basic assumptions about the patterns in community composition formulated from observations of current assemblages often cannot explain past community patterns (e.g., Jackson et al. 2001, Fox 2006).

One of the more striking pattern-based surprises in modern-day ecology was the discovery of deep ocean vent communities (Corliss et al. 1979, Grassle 1985, 1986). These communities have been increasingly well-studied following their discovery, but nearly every aspect of their existence has been surprising, in some cases even astonishing. The population densities, species composition, and in situ chemical energy source of these communities all contradicted universally accepted generalities about the ecology of deep ocean regions as low-density, low-productivity ecosystems reliant only on sparse detrital fallout from the distant photic zone.

Another example of a spatial surprise is the discovery of "fir waves," regions of high-elevation fir (*Abies* spp.) forests in both northeastern North America and Japan that show banded patterns of death and regeneration (Sprugel 1976, Sato and Iwasa 1993). The causes of this unusual large-scale patterning in forest structure were obscure at the time of discovery. Even after decades of work on fir waves, the relative importance of abiotic forces (wind and ice scour) vs. biotic factors is still not entirely clear (Shibuya et al. 2004).

Intervention-based surprises

One could argue that, more often than not, major human manipulations of natural communities produce

surprising, and sometimes even alarming, results (Paine et al. 1998). One of the most astonishing case studies we know involved an effort to reintroduce rock lobsters to a seamount off the western coast of South Africa (Barkai and McQuaid 1988). Until about 1970, similarly high population densities of rock lobsters (*Jasus lalandii*) reportedly occurred at Malgas and Marcus Islands, two closely associated and seemingly similar habitats. For reasons that remain uncertain, the lobsters disappeared from Marcus Island in the early 1970s. The lobsters preyed on predatory whelks and whelk populations apparently increased substantially following the lobsters' disappearance. After a 9-month caging experiment demonstrating that lobsters were indeed capable of surviving at Marcus Island, 1000 lobsters were reintroduced in an effort to reestablish the species. However, these lobsters were immediately attacked and consumed by their previous prey, the now overabundant whelks; a week later, live lobsters could not be found at Marcus Island (Barkai and McQuaid 1988). Such predator-prey role reversals were previously unknown and thus unexpected in this or any similar system.

Other examples of such unintended consequences of management actions are so pervasive that we simply list several here.

1) Indiscriminant control of coyotes can lead to identical or even higher livestock depredation rates, due to a variety of factors, including demographic responses, age- and individual-based differences in propensities to attack livestock, and differences in individual susceptibility to control measures (reviewed in Mitchell et al. 2004).

2) Control of red foxes in order to increase Red Grouse populations often backfires, with no reduction in numbers or increased cycling of grouse populations in areas with greater predator control. Foxes preferentially kill birds with higher parasite loads, and in the absence of predation, population-wide parasitism rates increase, with consequent negative impacts on grouse populations (Hudson et al. 1992, 1998, Packer et al. 2003).

3) Past efforts to remove cattle from California grasslands in order to help populations of native plants often failed because grazing suppressed the now widespread European grasses that strongly outcompete most native plants. Now, conservation easements stipulate both maximum and minimum levels of grazing in the hopes of improving native populations (Germano et al. 2001, Hayes and Holl 2003).

A structured questionnaire to assess ecological surprises

Although these examples give the sense that unanticipated ecological patterns and dynamics are common, such a listing clearly suffers from the problem of cherry picking. Thus, we also sought a somewhat more quantitative estimate of the frequency of ecological surprises. Given the nature of the peer-reviewed literature, which does not encourage the discussion, or even admission, of clearly unanticipated results, we

attacked this problem by constructing an extremely simple questionnaire (Appendix A), which we then sent to 115 experienced field ecologists. The list was generated in the following manner. First, members of our NCEAS working group listed the names of experienced field ecologists with medium- to long-term research programs whom we could recall from memory. We added to this list by searching the Web of Science for papers that contained "ecology" and "long-term" as key words. Finally, we added the names of any remaining field ecologists from the members list of the National Academy of Sciences. Our goal was simply to obtain a reasonably long list of credible field ecologists with enough experience to recognize an ecological surprise if they saw one.

After explaining our project and providing several well-known examples of ecological surprises, we asked the recipients whether or not they had encountered any such events in the course of their field studies, and if so, whether they believed that they were able to make a post hoc determination of the cause (see Appendix A). Fifty-eight (50%) of the 115 individuals contacted replied to our query within four weeks of the mailing. Fifty-two (90%) of the 58 respondents answered question 1 in the affirmative, five answered in the negative, and one was unable to make a determination based on the nature of his/her work. Of the 52 people responding in the affirmative, 46 (88%) believed that they understood the cause of the surprise after the fact. There were no substantial differences in the rate of affirmative vs. negative responses we received from researchers working predominantly in marine (14 affirmative out of 15 respondents), terrestrial (28 of 33), and freshwater (9 of 9) systems.

We draw two conclusions from this crude survey. First, major surprises are commonplace in the experience of field ecologists. If we assume the 58 respondents are a representative sample of reasonably competent field ecologists, nearly everyone experiences a significant surprise at one time or another over the course of their career. Even if we assume that the lack of responses were from those who have never been surprised, we would still conclude that a field ecologist would have an even chance of experiencing a surprise. Although these results do not allow us to estimate the relative fraction of surprising vs. expected results that these researchers have obtained during their careers, they do allow us to conclude that surprises are common enough to occur quite predictably in moderate- to long-term research programs. Second, and perhaps more interesting, was the fact that so many of those who have been surprised believed that they were able to make post hoc determinations of why the surprises occurred. This suggests that the factors responsible for surprises are easy to see but seldom anticipated. Ecological surprises thus occur because most ecologists have a predetermined notion of what they expect to see, and that this predetermined notion excludes many important ecolog-

ical processes. Finally, a surprising (to us) number of the respondents wrote to say that because their observations were surprises, they had not been reported in the scientific write-ups of their research, the implication being that these observations were uninteresting, bothersome, embarrassing, or not sufficiently well chronicled and understood through proper application of the scientific method, and thus were underreported in the scientific literature. The very fact that a result is surprising also means that a researcher will usually lack a clear and simple conceptual framework with which to introduce and discuss his or her results, making publication in most general ecology journals much more difficult.

WHAT CAUSES ECOLOGICAL SURPRISES?

Next, we present our view of why many surprises occur, while acknowledging that the diversity of these events makes such a classification difficult. Others have written about various ideas and phenomena relevant to what we term ecological surprises, especially their causes (Appendix B). Drawing on this literature and on our own discussions, we believe that there are four broad explanations for the majority of ecological surprises.

Complex community interaction webs.—Although lip service is routinely paid to the complexity of ecological communities, in fact almost all our expectations of community behavior come from highly simplified, cartoon versions of the myriad interactions that characterize real communities (Polis and Strong 1996). These cartoons rely (often implicitly) on several different assumptions that different camps of ecologists make about interaction webs: (1) bottom-up forces in communities dramatically outweigh all other effects; (2) top-down forces in communities dramatically outweigh all other effects; and (3) indirect interaction strengths rapidly attenuate with increasing interaction chain length, and thus ecological chain reactions are of minor consequence. In fact, real food webs are typified by many types of interactions. We do not agree with Polis and Strong (1996) that this complexity will always make simpler characterizations misleading or useless, but we do agree that it can produce results that are difficult to anticipate.

Variability in community players in time and space.—As with the complexity of species interactions, most ecologists appreciate that the numbers of individuals within populations, the traits of these individuals, and even the simple presence of different populations can vary dramatically across time and from place to place within otherwise similar communities. Despite this broadly held appreciation, predictions of future community and population behavior typically do not take the degree of this variability into account in any satisfying way. At the most basic level, genetic and behavioral differences between individuals of the same species mean that their roles in communities can vary both spatially and temporally (e.g., Agrawal 2003,

Thompson 2005). The most dramatic type of variation (and the most surprising in its effects) comes when species cross the boundaries between what we felt were distinct community or ecosystem types (Post et al. 2007). This inter-system connectivity not only is difficult to anticipate if one has not seen it before, but also can bring qualitatively different species into a community, with effects on existing players that are difficult to anticipate.

Multi-dimensionality of the characteristics and interactions of individual organisms.—The vast majority of formal ecological models and, we would argue, just as many informal mental models, reduce each species and individual to a simple set of characteristics and interaction rules. For example, in the typical Lotka-Volterra based models of interaction webs (e.g., May 1973, Laska and Wootton 1998, Wootton and Emerson 2005) each species is characterized by, at best, a birth rate, a death rate, and an interaction rate with each species it feeds on or is eaten by. Similarly, most models assume that biomass or energy is an adequate sole currency with which to characterize trophic interactions, ignoring the transfer of other major and minor elements and compounds. Although this reduction in the complex multidimensionality of a species' or individual's traits is necessary in order to achieve manageability within a single model, or human brain, it drastically curtails the full range of species complexities. There are many dimensions to the manner in which species interact with one another, including non-trophic interactions (facilitation, mutualism, etc.), behavioral effects (e.g., the ecology of fear; Berger et al. 2001, Laundre et al. 2001), stoichiometric effects (Sterner and Elser 2002), and trait-mediated indirect effects (e.g., Billick and Case 1994, Schmitz 1998, Hansen et al. 2007). Virtually none of these effects are typically incorporated into broad community predictions. Possibly just as important as its sheer complexity is that this multidimensionality makes interaction patterns context-dependent, changing with densities and community context and thus creating surprises such as the lobster-whelk role reversal previously described.

Shifting abiotic conditions can alter species reactions and interactions.—This last cause of surprises is really a small subset of the multi-dimensionality problem just discussed, but differs from it both in its current importance in the ecological literature (due to concerns with climate change) and because, more than the other causes we have listed, it is difficult to anticipate or predict with anything but long-term data. Both shifts in mean conditions and rare weather events can alter populations and communities in ways that are extremely difficult to anticipate. For example, would warming in Alaska lead to increased bark beetle outbreaks because of faster population growth of the beetle, or more control of beetle populations due to faster growth of their parasitoid enemies? Species can interact with one another in qualitatively or quantitatively different ways

depending upon variation in the physical conditions that surround them (e.g., Sanford 1999). The pattern of increasing variance in weather events at longer time scales has long been recognized as a source of uncertainty in ecological predictions (Pimm and Redfearn 1988), but increasing variability and shifting means due to global change now make prediction of the exact effects of climate change even more challenging (Boyce et al. 2006).

At a more fundamental level, we believe the various causes of ecological surprises can be divided into three categories of events: (1) those we just haven't seen and therefore don't know about, (2) those we have (or should have) observed but have overlooked due to failures of our imagination and intellect, and (3) those that we are well aware of, but have knowingly overlooked for logistical or intellectual simplicity and convenience. In other words, we are sometimes surprised because of ignorance, sometimes because of a failure to pay careful attention, and sometimes because we have to prioritize which aspects of ecology to include and which to ignore in order to make predictions. Different examples that we have mentioned here clearly fall into each of these three classes, but in many cases the line between things we don't know and those we do is not so clear, largely because of the limited scope, duration, and accuracy our observations. Recently, a great deal of work has been devoted to defining more explicitly and quantitatively how to include limited information in the formulation of predictions. We turn next to a discussion of the advances made in this field, but also why we do not feel that it can help with the most fundamental problems posed by ecological surprises.

CURRENT EFFORTS TO IMPROVE PREDICTIONS, QUANTIFY UNCERTAINTY, AND AVOID SURPRISES

Over the past two decades, ecologists, resource managers, and statisticians have become increasingly interested in the quantification and presentation of uncertainty in ecological predictions. Much of this work has been directly tied to conservation or resource management, areas where medium- to long-range predictions are routinely made, often with little acknowledgement of uncertainty. Our interest in this body of theory arises because better specification of the uncertainty in ecological predictions would seem to offer a way to mitigate the problem of ecological surprises; if we can make clear statements about the uncertainty in our expectations, we should not be surprised by nearly as many outcomes, because most will fall within the (presumably broad) range of possible predictions.

Major foci of this emphasis in applied ecology have been the inclusion of abiotic variance in models of population and community dynamics (e.g., Coulson et al. 2001, Hallett et al. 2004, Smith et al. 2005), the use of statistics of extremes to predict rare events (Gaines and Denny 1993, Moritz 1997, Ellison and Agrawal 2005), and the promotion of both information-theoretic and

Bayesian methods to quantify and emphasize the uncertainty that arises from different predictive model structures and individual parameter values (Hilborn and Mangel 1997, Burnham and Anderson 2002, Link et al. 2002, Spiegelhalter et al. 2002, Johnson and Omland 2004). In addition, there is a developing literature on general approaches to uncertainty and how best to regard uncertainty and its sources, a literature that includes elements of both statistics and larger considerations about the basis for knowledge and decision making (Regan et al. 2002). All of these approaches offer ways to classify sources of uncertainty, and in particular they all emphasize the many different types of uncertainty that can or should be considered when making predictions.

Of these areas of emphasis, the most influential to date have been the ones, such as Bayesian modeling and AIC-based model evaluation, that offer formal, clearly defined ways to incorporate important types of uncertainty into predictive models. Use of these analytical tools has already provided critical improvements in ecological modeling and prediction. However, we would argue that these methods can do relatively little to change the frequency or magnitude of ecological surprises. These methods are, for the most part, ways to quantify and highlight well-known and prosaic sources of errors: in a word, a means of keeping track of the errors we already know about. This is not to undervalue this care and precision; it is very important to emphasize the lack of clarity that most predictions about ecological patterns and management outcomes will have. However, tools that can quantify a broader range of "not surprising" results than usually acknowledged are different from a method that would allow us to anticipate what are now surprising outcomes. The uncertainties that come out of a careful analysis of likely management actions are always minimum estimates, explaining only the uncertainties and processes modeled. Although this caveat has been made quite forcefully by the most influential authors advocating better ecological model testing (e.g., Hilborn and Mangel 1997, Burnham and Anderson 2002), this caution is not always reflected in the use and presentation of these analyses by other practitioners. Real variation is often (perhaps even typically) far in excess of these predicted minima, and will arise from sources that are difficult or impossible to quantify using these methods, even in well-studied systems. Hence, "surprises" are seen quite commonly even in exceptionally well-studied ecosystems.

SUMMARY: USING IMAGINATION AND HUMILITY IN ECOLOGICAL FORECASTING

Cognitive psychology has convincingly shown that humans are pattern-recognition machines, looking for consistency and predictability even when it does not exist. We tend to perceive consistency and hence predictive strength even when little pattern or causality can objectively be found (Gilbert 2006). This tendency is

especially evident in ecological research and applied conservation management, where future expectations are typically based on two general approaches: expert opinions and simple conceptual or mathematical models (see Egerton [1973] for a classic exploration of the balance of nature concept). Using these approaches, ecologists have tended to seek and see broad patterns and to make predictions with a great deal of confidence. The appeal of simple, deterministic models, even when we know that they are rarely correct, may lie in part in their ability to generate far broader, less conditional, predictions than do more complicated nonequilibrium analyses. And those experts who make the strongest arguments, even if wrong, tend to be the most influential, at least in the short term. However, the work by Tetlock (2005) on expert opinion suggests that simply accepting forceful expert opinions is even more dubious than it at first appears. In a very different field (international politics), he finds that experts with the most confidence in their predictions also made the worst predictions, at least in part because they were least willing to change their theories in the face of conflicting information. Although formal risk assessment methods can be used to tease out more reliable information from groups of expert opinions, they are little used in applied ecology.

Perhaps this recognition of general human frailties makes the high frequency of ecological surprises more understandable. Ecologists study extraordinarily complex systems, they base their expectations on limited data that are frequently of short duration, and they are, after all, only human. But these comforting words are likely to make many ecologists (like other experts) hear an inner voice that says, "Maybe so, but I am not stupid, like those other ecologists, who apparently didn't really know their study systems." To this natural reaction, we would answer: those who think that their study systems have ambushed or bamboozled them—really surprised them—include many of the most accomplished living ecologists. For example, all 10 of the National Academy members who answered our survey agreed that they had seen ecological surprises in their field systems.

If even the best ecologists are rather poor at anticipating the behavior of extremely well-studied ecological systems, what does this suggest about ecological research and about the conservation and management of natural populations and communities? For basic research, it implies that there is much to learn, even about ecological systems that seem to have been studied to death. In this regard, the frequency of ecological surprises is a further justification for the recent expansion of long-term ecological monitoring and research programs (e.g., NSF's LTREB, which recognizes the leading role of long-term, individual-investigator research programs in probing ecological dynamics, as well as the LTER, NEON, and numerous governmental monitoring programs; see Lovett et al. 2007; Billick and Price, *in press*). Our four general explana-

tions for surprises comprise a set of possible foci for more research into community dynamics, and they imply the need for greater integration of complexity into the models we use to make predictions and greater imagination in our formulation of ecological expectations.

The frequency of ecological surprises also has two major implications for natural resource management. First, it implies that most management strategies, sooner or later, will not work as planned. In many resource management fields, there is recognition that some form of adaptive management is needed to respond to and learn from changing conditions and expanding understanding (Holling 1978, Walters and Hilborn 1978, Bormann et al. 1994, Gunderson and Light 2006). This philosophy accords well with the recognition that our management strategies are sometime not just less than perfect in achieving some desired outcome, but totally wrong. However, an equally strong trend in natural resource management has been the desire to put into place fixed, unchanging management strategies that will not "surprise" business interests (Baur and Donovan 1997, Wilhere 2002). Strategies of this nature are clearly not consistent with the true uncertainty in our ecological models and management plans; the recognition of how common surprises are suggests the need for more active, scientifically based opposition to this trend in environmental management, rather than acceptance of rigid management rules as a political necessity.

Second, frequent ecological surprises reinforce the need for management plans that are highly precautionary, rather than ones that attempt to cut close to expected thresholds of population overexploitation or community collapse. The precautionary principle has enjoyed periods of both popularity and neglect in academic circles, but any systematic application of this idea has been opposed by political and business forces that generally view it as expensive at best and heretical at worst (Raffensberger and Tickner 1999, Sunstein 2005; but see Hammill and Stenson 2007). Again, documentation of the frequency of ecological surprises provides a clear and rational basis for precautionary management strategies. Together, these two conclusions indicate that ecological management should remain flexible and that it should be even more precautionary than suggested by formal analysis. In the inevitable disagreements over the best way to balance the costs of management with the needs of populations and communities, the recognition of ecological surprises as a demonstrable fact can lend support to better and more conservative planning.

Surprises also suggest that cross-systems analysis is likely to be highly valuable. Experts in any area of knowledge become entrenched in their ideas and share familiarity with the same data sets and theories. In our experience, discussion and review between system-specific experts and those who are knowledgeable outsiders can be invaluable, especially because outsiders will question assumptions and be more open to

alternative mechanisms because of their experiences in other ecological communities. Specifically, this suggests that Endangered Species Act recovery teams, National Research Council committees, and similar peer review bodies should make a point of including not just system-specific scientists, but also researchers with quite different experiences: outsiders who can and will look at a system or problem with fresh eyes.

Finally, we wish to emphasize that there are two conclusions that we do not draw from our analysis of ecological surprises. The frequency of surprises could be used to argue that trying to understand ecological dynamics is largely a useless exercise. We certainly do not agree with this assessment. Rather, we believe that the progress ecologists have made in predicting short-term and "normal" patterns of ecological systems should be applauded, but also tempered with modesty about our larger predictive power and ability to understand complex systems. Practices in the field of financial investing provide a good analogy to the stance we suggest for ecological predictions. A great deal of money and effort has been used to model the best ways to maximize investment returns (certainly more money and effort than has been used to refine ecological predictions). Although this work has resulted in greatly increased understanding of economic systems, the risks and limitations of using sophisticated economic models to make investments has led more and more investors to instead use simple, safe index funds. Essentially this is the recognition that the models and expert opinions are of exceptionally little value in making accurate, long-range predictions in this field and that precautionary strategies are a far better alternative.

A second possible conclusion could be that only by formulating far more complex models can we improve our understanding of ecological systems. Again, we would disagree with this conclusion. Understanding and prediction of ecological processes will undoubtedly benefit from more analysis and more long-term data collection on difficult and unclear effects. Furthermore, the trend away from single-species management planning to the consideration of ecosystem and community dynamics is likely to provide more accurate, less surprising outcomes. But one of the best features of the recent blooming of information theory and Bayesian methods in ecology has been the decline in building elephant-sized models on the backs of mouse-sized data sets. As most ecologists now realize, AIC methods and their kin routinely show that when data are limited, formal predictive models should be simple. We should keep our minds open to more complex effects, but concentrate first on obtaining data to test these effects, instead of rushing to parameterize guesses and hunches.

Ecological surprises appear to be all but inevitable, and there is no indication that this situation will change any time soon. As we have stated here, this suggests that we proceed cautiously and adaptively when making management plans, and when advancing broad gener-

alities about ecological structures and processes. This entire message might seem defeatist, but we have found it the opposite in our own discussions. Surprises suggest that many features of individuals, populations, and communities we usually overlook are in fact important in generating the dynamics we wish to understand. This is a scientifically interesting and challenging conclusion, and if recognizing this complexity can avert at least some future management fiascos, then we consider it a useful change in our perceptions of ecological understanding as well. Thus, while we should proceed with humility with prediction and management of ecological systems, we should also recognize the challenge that surprises represent to our understanding and respond with renewed efforts to creatively disentangle the complexity of our study systems

ACKNOWLEDGMENTS

This paper arose from our discussions during the "Conservation Planning for Ecosystem Functioning: Testing Predictions of Ecological Effectiveness for Marine Predators" working group at the National Center for Ecological Analysis and Synthesis. Craig Osenberg contributed to our discussions. Keith Miles, Mark Ricca, Pete Holloran, members of the Doak lab meeting, and two anonymous reviewers provided valuable comments on the manuscript. Finally, we offer our greatest thanks to the many ecologists who took the time and care to answer our out-of-the-blue questionnaire regarding their research experiences.

LITERATURE CITED

- Agrawal, A. A. 2003. Community genetics: new insights into community ecology by integrating population genetics. *Ecology* 84:543–544.
- Barkai, A., and C. McQuaid. 1988. Predator–prey role reversal in a marine benthic ecosystem. *Science* 242:62–64.
- Baur, D. C., and K. L. Donovan. 1997. The no surprises policy: Contracts 101 meets the Endangered Species Act. *Environmental Law* 27:767–790.
- Berg, E. E., J. D. Henry, C. L. Fastie, A. D. De Volder, and S. M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227:219–232.
- Berger, J., J. E. Swenson, and I. L. Persson. 2001. Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036–1039.
- Billick, I., and T. J. Case. 1994. Higher-order interactions in ecological communities: What are they and how can they be detected? *Ecology* 75:1529–1543.
- Billick, I., and M. Price, editors. *In press*. The ecology of place. University of Chicago Press, Chicago, Illinois, USA.
- Bormann, B. T., P. G. Cunningham, M. H. Brookes, V. W. Manning, and M. W. Collopy. 1994. Adaptive ecosystem management in the Pacific Northwest. General Technical Report PNW-GTR 341. USDA Forest Service, PNW Research Station, Portland, Oregon, USA.
- Boyce, M. S., et al. 2006. Demography in an increasingly variable world. *Trends in Ecology and Evolution* 21:141–148.
- Brown, J. H., and E. J. Heske. 1990. Control of a desert–grassland transition by a keystone rodent guild. *Science* 250:1705–1707.
- Burnham, K., and D. Anderson. 2002. Model selection and multi-model inference. Springer-Verlag, New York, New York, USA.

- Carpenter, S. R. 2003. Regime shifts in lake ecosystems: pattern and variation. Volume 15. Excellence in Ecology Series. Ecology Institute, Oldendorf/Luhe, Germany.
- Corliss, J. B., J. B. Dymond, L. I. Gordon, J. M. Edmond, R. P. V. Herzen, R. D. Ballard, K. Green, D. Williams, A. Bainbridge, K. Crane, and T. H. Vanandel. 1979. Submarine thermal springs on the Galapagos Rift. *Science* 203:1073–1083.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292:1528–1531.
- Davis, M. B. 1969. Climatic changes in southern Connecticut recorded by pollen deposition at Rogers Lake. *Ecology* 50:409–422.
- Doroff, A. M., J. A. Estes, M. T. Tinker, D. M. Burn, and T. J. Evans. 2003. Sea otter population declines in the Aleutian Archipelago. *Journal of Mammalogy* 84:55–64.
- Egerton, F. N. 1973. Changing concepts of the balance of nature. *Quarterly Review of Biology* 48:322–350.
- Ellison, A. M., and A. A. Agrawal. 2005. The statistics of rarity. *Ecology* 86:1079–1080.
- Estes, J. A., E. M. Danner, D. F. Doak, B. Konar, A. M. Springer, P. D. Steinberg, M. T. Tinker, and T. M. Williams. 2004. Complex trophic interactions in kelp forest ecosystems. *Bulletin of Marine Sciences* 74:621–638.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking coastal with oceanic ecosystems. *Science* 282:473–476.
- Fox, D. 2006. Dig deeper. *Conservation in Practice* 7:14–21.
- Frost, T. M., J. M. Fischer, J. L. Klug, S. E. Arnott, and P. K. Montz. 2006. Trajectories of zooplankton recovery in the little rock lake whole-lake acidification experiment. *Ecological Applications* 16:353–367.
- Gaines, S. D., and M. W. Denny. 1993. The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecology* 74:1677–1692.
- Genkai-Kato, M. 2007. Regime shifts: catastrophic responses of ecosystems to human impacts. *Ecology Research* 22:214–219.
- Germano, D. J., G. B. Rathbun, and L. R. Saslaw. 2001. Managing exotic grasses and conserving declining species. *Wildlife Society Bulletin* 29:551–559.
- Gilbert, D. 2006. *Stumbling on happiness*. Alfred A. Knopf, New York, New York, USA.
- Grassle, J. F. 1985. Hydrothermal vent animals: distribution and biology. *Science* 229:713–717.
- Grassle, J. F. 1986. The ecology of deep-sea hydrothermal vent communities. *Advances in Marine Biology* 23:301–362.
- Gunderson, L., and S. S. Light. 2006. Adaptive management and adaptive governance in the Everglades ecosystem. *Policy Sciences* 39:323–334.
- Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and B. T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* 430:71–75.
- Hammill, M. O., and G. B. Stenson. 2007. Application of the precautionary approach and conservation reference points to management of Atlantic seals. *Journal of Marine Science* 64:702–706.
- Hansen, D. M., H. C. Kiesbuy, C. G. Jones, and C. B. Muller. 2007. Positive indirect interactions between neighboring plant species via a lizard pollinator. *American Naturalist* 169:534–542.
- Hayes, G. F., and K. D. Holl. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* 17:1694–1702.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, New Jersey, USA.
- Holling, C. S., editor. 1978. *Adaptive environmental assessment and management*. John Wiley, London, UK.
- Hudson, P. J., A. P. Dobson, and D. Newborn. 1992. Do parasites make prey vulnerable to predation? Red grouse and parasites. *Journal of Animal Ecology* 61:681–692.
- Hudson, P. J., A. P. Dobson, and D. Newborn. 1998. Prevention of population cycles by parasite removal. *Science* 282:2256–2258.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.
- Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19:101–108.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. *North American Fauna* 68:1–352.
- Laidre, K. L., J. A. Estes, M. T. Tinker, J. Bodkin, D. Monson, and K. Schneider. 2006. Patterns of growth and body condition in sea otters from the Aleutian archipelago before and after the recent population decline. *Journal of Animal Ecology* 75:978–989.
- Laska, M. S., and J. T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* 79:461–476.
- Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79:1401–1409.
- Link, W. A., E. Cam, J. D. Nichols, and E. G. Cooch. 2002. Of BUGS and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management* 66:277–291.
- Lovett, G. M., D. A. Burns, C. T. Driscoll, J. C. Jenkins, M. J. Mitchell, L. Rustad, J. B. Shanley, G. E. Likens, and R. Haeuber. 2007. Who needs environmental monitoring? *Frontiers in Ecology and the Environment* 5:253–260.
- Matsuoka, S. M., E. H. Holsten, M. E. Shephard, R. A. Werner, and R. E. Burnside. 2006. *Spruce beetles and forest ecosystems of south-central Alaska: Preface*. *Forest Ecology and Management* 227:193–194.
- May, R. M. 1973. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Mitchell, B. R., M. M. Jaeger, and R. H. Barrett. 2004. Coyote depredation management: current methods and research needs. *Wildlife Society Bulletin* 32:1209–1218.
- Monson, D., J. A. Estes, D. B. Siniff, and J. B. Bodkin. 2000. Life history plasticity and population regulation in sea otters. *Oikos* 90:457–468.
- Moritz, M. A. 1997. Analyzing extreme disturbance events: fire in Los Padres National Forest. *Ecological Applications* 7:1252–1262.
- Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15:232–237.
- Packer, C., R. D. Holt, P. J. Hudson, K. D. Lafferty, and A. P. Dobson. 2003. Keeping the herds healthy and alert: implications of predator control for infectious disease. *Ecology Letters* 6:797–802.
- Paine, R. T., M. J. Tegner, and A. E. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1:535–545.
- Pimm, S. L., and A. Redfearn. 1988. The variability of animal populations. *Nature* 334:613–614.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- Post, D. M., M. W. Doyle, J. L. Sabo, and J. C. Finlay. 2007. The problem of boundaries in defining ecosystems: a potential landmine for uniting geomorphology and ecology. *Geomorphology* 89:111–126.

- Raffensberger, C., and J. Tickner, editors. 1999. Protecting public health and the environment: implementing the precautionary principle. Island Press, Washington, D.C., USA.
- Regan, H. M., M. Colyvan, and M. A. Burgman. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications* 12:618–628.
- Reisewitz, S. E., J. A. Estes, and C. A. Simenstad. 2006. Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. *Oecologia* 146:623–631.
- Roemer, G. W., C. J. Donlan, and F. Courchamp. 2002. Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences (USA)* 99:791–796.
- Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283:2095–2097.
- Sato, K., and Y. Iwasa. 1993. Modeling of wave regeneration in sub-alpine *Abies* forests: population dynamics with spatial structure. *Ecology* 74:1538–1550.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folkes, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8:275–279.
- Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* 151:327–342.
- Shibuya, M., N. Haga, T. Sasaki, S. Kikuchi, M. Haruki, M. Noda, K. Takahashi, and K. Matsuda. 2004. Stand and self-thinning dynamics in natural *Abies* stands in northern Hokkaido, Japan. *Ecological Research* 19:301–309.
- Smith, M., H. Caswell, and P. Mettler-Cherry. 2005. Stochastic flood and precipitation regimes and the population dynamics of a threatened floodplain plant. *Ecological Applications* 15:1036–1052.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society B* 64:583–639.
- Sprugel, D. G. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. *Journal of Ecology* 64:889–911.
- Sturner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, New Jersey, USA.
- Sunstein, C. R. 2005. *Laws of fear: Beyond the precautionary principle*. Cambridge University Press, Cambridge, UK.
- Tetlock, P. E. 2005. *Expert political judgment: How good is it? How can we know?* Princeton University Press, Princeton, New Jersey, USA.
- Thompson, J. N. 2005. *The geographic mosaic of coevolution*. University of Chicago Press, Chicago, Illinois, USA.
- Walters, C. J., and R. Hilborn. 1978. Ecological optimization and adaptive management. *Annual Review of Ecology and Systematics* 9:157–188.
- Watt, J., D. B. Siniff, and J. A. Estes. 2000. Interdecadal change in diet and population of sea otters at Amchitka Island, Alaska. *Oecologia* 124:289–298.
- Wilhere, G. F. 2002. Adaptive management in habitat conservation plans. *Conservation Biology* 16:20–29.
- Wolda, H. 1978. Fluctuations in abundance of tropical insects. *American Naturalist* 112:1017–1045.
- Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. *Annual Review of Ecology Evolution and Systematics* 36:419–444.
- Young, T. P. 1994. Natural die-offs of large mammals: implications for conservation. *Conservation Biology* 8:410–418.

APPENDIX A

Questionnaire that was e-mailed to 113 experienced field ecologists (*Ecological Archives* E089-056-A1).

APPENDIX B

Past conceptual work related to ecological surprises (*Ecological Archives* E089-056-A2).