Citations, anonymous ideas, and ecological engineering

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We were both surprised in our first encounters with Larry Slobodkin. When Lev Ginzburg first came to Stony Brook on a job interview in 1977, he was startled to meet Slobodkin who, he had assumed from his publication record, must have been dead, or at least over 80 years old. In fact, he was under 50 at the time. Slobodkin has several papers that have been cited thousands of times, which is really remarkable in a relatively small field like ecology. Slobodkin's impact on the discipline has been pervasive and profound, yet often anonymous. Many of his ideas have already been integrated into the fabric of ecology in a way that no longer requires citation. They have become anonymous ideas. When Scott Ferson came to study at Stony Brook in 1980 as a first-year graduate student, he had an initially negative impression from reading Slobodkin's 1961 book Growth and Regulation of Animal Populations. He thought the book highly derivative and even hackneyed because it just recounted what everyone knows about ecology. It took a while for him to realize that everyone in ecology knew these things precisely because Slobodkin's book had introduced them to the field. In the Russian language, a similar fate of integration befell Griboyedov's play Woe from Wit, which, when read today by the young, seems like a collection of standard metaphors and turns of phrase they've grown up hearing. It was hard to fathom how novel the ideas were when he wrote them because they are so second-nature today. Because Slobodkin's ideas were so obvious and natural and true, one would think we've just always had them.

We would like to trace the origin and flowering of one idea of Slobodkin's that is so useful and natural that it has become nearly anonymous today. A quarter century ago, Slobodkin and Ginzburg worked with graduate students Keith Johnson and Andrew Bindman on a paper that introduced the notion of quasi-extinction risk, that is, the probability that a biological population falls below some threshold level (Ginzburg et al. 1982). This idea is fundamental in both ecological risk analysis (Barnthouse and Suter 1986; Suter 1993; 1996a; 1996b; Warren-Hicks and Moore 1998; Akçakaya et al. 2008) and quantitative conservation biology (Burgman et al. 1993; Akçakaya et al. 1999; Ferson and Burgman 2000; Morris and Doak 2002; Akçakaya et al. 2004), which are two environmental engineering disciplines growing from the science of ecology. It also provides a basic context for modern probabilistic incarnations of wildlife management and the stock assessment methods of fisheries biology.

To compute the risk of extinction or population decline, one needs models of stochastic population growth responding to environmental variation that are detailed enough to include demographically important features of population biology. In a sense, such models represent a synthesis that unifies the two schools of thought about what regulates growth of populations. The first school of thought, long championed by Slobodkin's teacher G. Evelyn Hutchinson as well as Slobodkin and many of their

colleagues, holds that it is primarily biological feedbacks, collectively called density dependence, that prevent long-term exponential growth of a population into a Malthusian explosion (Elton 1927; 1949; Nicholson 1933; 1957; Hutchinson 1948; Hairston et al. 1960; Slobodkin 1961). The competing school of thought, championed by the Australians H.G. Andrewartha and L.C. Birch and their colleagues, held that stochastic events in the natural environment are the primary check on exponential growth (Andrewartha and Birch 1954). The debates between these two schools of thought organized much of animal ecology during of the last century, and were as important as the concurrent Clements-Whittaker debate in plant community ecology. It is fitting that their resolution and final unification spawn the highly quantitative disciplines that will dominate applied ecology in the coming decades.

Quasi-extinction risk is the probability that a population will fall below some critical threshold abundance within a specified time horizon. It generalizes the risk of extinction which is a special case where that threshold is zero. It also generalizes the risk of population decline where the magnitude of the decline can be expressed in absolute terms or relative to the initial abundance. We use the word quasi-extinction to refer to all of these probabilities considered collectively as functions of all the thresholds or time horizons of interest. Quasi-extinction is thus a far richer characterization of the prospects for a population than any of the simple population summaries that are often used by academic biologists, including current population size, population growth rate, and λ (the eigenvalue associated with the population growth equation, Caswell 1989). It tells us how likely each of the possible fates of a population is. Such information is crucial to forecasting the likely consequences on the population from harvesting or some environmental impact, planning remediation efforts, developing restocking schemes, comparing different management strategies, and determining whether an impact will have tolerable incremental risks for the population. It is, in short, fundament for ecological engineering. The original paper developed graphical depictions for displaying risks that are still used today. It also argued that the risk language was needed to express and solve ecological problems. In only this probabilistic language, can we properly contextualize impacts and stresses against population variation arising from natural environmental stochasticity. This is an important advantage from the perspective of an ecologist, for whom, as Simberloff quipped, the noise is the music. We cannot ignore the variation; we must understand it.

The formula for quasi-extinction accounts for the continual and sometimes violent fluctuations that Andrewartha and Birch observed in the numbers of individuals in populations, and it also accounts for the biological feedbacks manifested in the species' population biology. Quasi-extinction risk depends on the population threshold and the time horizon, but also on the population's initial abundance and its biology within its environment. Because the natural environment is almost always fluctuating through time, population growth is a stochastic process. Favorable years tend to produce good growth, and less favorable years tend to result in less growth, or even reductions in the population. The environmental fluctuations are caused by variation in numerous abiotic and biotic factors such as the weather, habitat and breeding site availability, food supply, predators, pests and pathogens. Because the dynamics of these factors cannot be precisely predicted, biologists cannot really foretell whether any given year will be favorable or unfavorable. However, we can build probabilistic models of past weather patterns, variation in food supply, etc., and incorporate any projected trends such as climate change, habitat loss, and other temporal patterns, and use these models to make ensemble predictions about the population's future. This approach allows ecological engineers to represent in a realistic way the ubiquitous variability that is the often most salient feature of population dynamics of species in the real world. Of course, even highly stochastic models require some form of density dependence to prevent the emergence of unrealistic patterns of exponential growth in the long term. The biology of the population may manifest density-dependent feedbacks such that population growth rate depends on the population's current density. As a first approximation, the formulation uses a simple generalization of the logistic model of density dependence.

The quasi-extinction formula developed in Ginzburg et al. (1982) is a solution to what mathematicians call a first passage time problem because it concerns the event in which a population trajectory first crosses some threshold abundance. Expressions for the density have been known in physics for some time, but our application required an expression for the cumulative probability. Essentially the same formula for computing quasi-extinction risk was apparently independently discovered by Lande and Orzack (1988). They pointed out that its symmetry makes it useful for characterizing the chance of population growth as well as the risk of population decline. The formula for quasi-extinction was apparently rediscovered a second time by Morris and Doak's (2002) who even depicted it on the cover of their textbook on quantitative conservation biology

(http://www.amazon.com/gp/reader/0878935460/ref=sib_dp_pt#reader-link). If it is true, as editors say, that every equation in a book cuts its sales by half, it is surely a testament to the importance of the notion of quasi-extinction that the authors would hazard to display its formula on the cover. Interestingly, none of these discoveries was actually the first. It turns out that the same formula was also derived in the 1970s as a part of work by econometricians on stochastic-price equity markets for which Merton and Scholes received the 1997 Nobel Prize in Economics.

The formula itself is nice and helpful for developing intuition, but it is of limited use in practice because its assumptions are rarely perfectly met. For instance, although it allows logistic density dependence, the carrying capacity is a constant, non-stochastic value, which would not always be realistic. Moreover, some populations exhibit other kinds of density dependence such as Ricker or Beverton-Holt. The model also lacks age and stage structure. If environmental fluctuations affect different age classes or demographic stages differently, then demographic pulses may occur that the formula cannot account for. The model also assumes no emigration, Allee effects, or harvesting, and that the probability distributions of parameters are stationary, so it cannot account for any long-term trends in the factors that determine growth. More flexible software that can take account of these complexities is needed for practical applications. Resit Akcakaya and Ferson at Ginzburg's company Applied Biomathematics developed several such software packages over the last two decades under the name RAMAS (Ferson and Akçakaya 1988; Akçakaya and Ferson 1990; Ferson 1990; Akçakaya 1997; Spencer and Ferson 1997a; 1997b; Akçakaya et al. 1999; Akçakaya et al. 2001; Akçakaya and Root 2003; Akçakaya 2005). There are also several similar software packages such as Vortex (Lacy 1993) and others (see Lindenmayer et al. 1995; Brook et al. 1999). Most of the packages model various forms of density dependence arising from the species' population biology, migration, harvesting, and the demographic structure of the population itself including age- or stage-structure (Burgman et al. 1993; Engen et al. 2002). Some of the packages model the spatial distribution of metapopulations (Akçakaya et al. 2008).

There have been hundreds of published applications of the RAMAS software to population viability analyses and other species-specific models of plants, invertebrates, fishes, amphibians, reptiles, birds, and mammals (see http://www.ramas.com/ramasapp.htm). The real importance of the formula and the approach based on quasi-extinction developed in 1982 is that they are antecedents of the books and these publications that are helping to shape the disciplines of ecological engineering, even though few of them actually cite the original paper.

Conventional wisdom suggests it is young scientists who are most concerned about their citation rates, although in truth it is older scientists who are especially sensitive to such matters. There are of course a couple of well known tricks for upping one's citation rates. One way is to publish methods papers. The other way is to publish controversial ideas. It is contentious ideas are still cited long after they are introduced, as if to blame the original author for any controversy they still engender. Ideas that are simply true are adopted and fairly quickly integrated as common intellectual property. The more natural the idea, the easier it is for anonymity to envelop it. This may suggest that, for the sake of one's citation record and fame within the discipline, it is better to be interesting than it is to be right. It is noteworthy that Slobodkin never fell into this trap of cynicism. Because environmentalism gained currency and political importance during his career, there were certainly opportunities for him to stray from scientific ecology to augment his stature. It seems that he never really understood the impulse to do so. He was always personally interested in the truth about the world, and not so much in notoriety or what it could bring him. He was never splashy, and he never seemed motivated by careerism. He always was and still is simply fascinated by the ideas in ecology.

Scientists are supposed to be dispassionate about ideas, but everyone knows this is a lie. Ideas are like children to a scientist, and, in a sense, an idea is a scientist's child, the progeny that expresses the contribution he or she makes to the future. Without commenting on Dawkins' theory of memetic evolution, we can speak at least metaphorically of a scientist's reward being to stay in the game, that is, for his ideas to stay relevant, perhaps spawning news ideas or recombining with ideas of other scientists. It is not surprising that we can become emotionally invested in our ideas, which we guard and foster in the hopes they develop. People outside the arts and sciences often do not understand this attachment that creative people have with ideas. Ideas are not merely mechanisms by which a scientist gets ahead. They are expressions of ourselves, encapsulations of our ingenuity. A scientist will have many ideas, but each of them is dear as a child. Infant mortality is very high. Almost all die, many smothered by scoffing colleagues around the lunch table or on the list server.

Concern about citations and credit is not limited to mean intellects. Arnold (1990) described Isaac Newton's petty fighting over scientific priority and his begrudging citations of Hooke (e.g., burying him in the middle of a list of citations). Newton himself argued that people who pretend that they don't care about such concerns are being dishonest, the evidence of which is the fact that they put their names on papers. He suggested that people who don't care about the credit should publish anonymously.¹ It is interesting that, in recent years, anonymous or pseudonymous publication has

¹ Newton himself occasionally misused anonymity. For instance, he anonymously reviewed his own work, and used anonymous publications in his disputes waged against Leibniz.

exploded, not in the respectable scientific literature, but on the internet's blogosphere. At the same time, however, ethical standards at several journals have been reviewed or tightened to require the disclosure of the actual authors and the sources of their support. Although consultants sometimes argue that it shouldn't matter where an idea comes from, that evidence is evidence no matter who paid for its collection and that a scientific publication deserves to be evaluated on its own merits, it is clear from recent scandals that allowing scientists to publish without properly acknowledging their own authorship can have adverse effects. For instance, it masks responsibility and obscures the motivations and predilections of the authors, and therefore stifles exegesis and confuses the understanding readers might otherwise have of the text.

Of course, anonymous gifts are considered the purest form of philanthropy. Scientists may not ethically make contributions anonymously, but their contributions can and do descend to anonymity if they are natural and true. In a sense, using a scientist's ideas even after the papers are no longer cited is the highest form of compliment within science. It implies that the ideas have become integral parts of the discipline and, thus, are *beyond* citation. Such ideas represent a pure contribution to science, untethered to fame or any name. They are children that never die. Slobodkin's contribution was one of a few seminal papers in the early 1980s that helped to start the fields of ecological risk analysis and quantitative conservation biology. It will soon become anonymous as its arguments and methods pervade the basic thinking and analyses in these fields.

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