Forty-eight Parrots and the Origins of Population Viability Analysis

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My unpaid postgraduate research associate raised his voice. "Forty-eight?" I looked up from my *Drosophila*. He said it strangely, almost ominously. It wasn't the universal and galactic 42, but 48, a somewhat larger number. And, I soon learned, it had more to do with the mathematics of Australian parrots than with the labored calculations of mice (c.f., *The Hitchhiker's Guide to the Galaxy*).

The postgraduate researcher was more interested in chaparral bird species in remnant habitats in the city of San Diego, where he had grown up, the local environment for our urban university. He had been interrupted from his maps and aerial photos. The question had arrived long distance from concerned scientists in Australia. They had only 48 parrots left; was it hopeless? Should they spend their limited resources elsewhere? They had phoned my postdoctoral associate to find out. With his permission, they might decide to let the parrots go extinct.

I hear him say something to the effect that there are no hopeless cases, only cases of people without hope. They should not despair. But from the tone in his voice I could tell he wasn't satisfied with that response. Forty-eight troubled him. The phone call was not concluded on an optimistic note.

Still mumbling "forty-eight," he returned to the table next to mine. "They've only got 48 parrots and they wonder if it is genetically hopeless to try to save them." It was nonsense to think that. He knew it and I immediately visualized a stochastic population growth line that happened to drop below 48 but then turned upwards. However, 48 was less than 50, and 50 was the rule, the Magic Number, the scientifically honed edge of the decision ax. And what's the point of rules if we don't follow them?

Was the rule wrong? It wouldn't have bothered me much if it was, but my postdoctoral associate was the author of the rule, a rule he had offered the world with the best of intentions, a rule to protect the single-species pieces of biodiversity. He was not amused to find the rule could be viewed as having two edges.

Through the next year, over coffee and at the black board, he and I wrestled with the implications of this and like rules, coming up with a new approach that turned away from minimum viable population level rules, with their possible dangers, and led us to publish a joint paper on the processes of population extinction wherein we introduced the concept of population viability analysis, PVA, a comprehensive process that evaluated extinction probabilities over different time frames. During this time, my postdoctoral associate had secured a half-time job at the University of Michigan, though he continued to spend most of his time in San Diego. One of his duties at Michigan was to organize workshops and meetings in the emerging area of conservation biology. In 1985 I presented our resulting PVA (Gilpin & Soulé 1986) paper at a meeting he organized: the Second International Conference on Conservation Biology. The talk went well. I'll never forget how Hal Salwasser ran up to me after the talk and enthusiastically told me that we finally "had it"—the "it" for him being the answer to the problem of the Northern Spotted Owl, which for him, as Deputy Chief of the U.S. Forest Service (USFS), was growing more vexing.

There are a lot of stories here. Why was Michael Soulé, who had hired me a decade earlier, working unpaid in my biology lab in the University of California, San Diego, in the early 1980s? This paradox has something to do with a different paradox, a Zen koan: whether dogs have Buddha Nature. It also has to do with collegiality and the fellow feeling of my department's more numerically dominant molecular biologists. And it has to do with retirement and rebirth.

The First International Conference of Conservation Biology had been held in 1978, a couple of buildings away from my lab and from the adjacent lab he had occupied. Based on a view of nature confined to reserves smaller than the area threshold for autochronous evolution, the end of evolution had been announced. And two genetic thresholds had been stated. A population of less than 50

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would go extinct in the short term due to inbreeding depression. And a size less than 500 would doom a species to adaptive rigidity and ultimate extinction in the face of environmental change.

One of the 1978 conference's organizers, Bruce Wilcox, had finished his Ph.D. and had left San Diego. The other organizer, Michael Soulé, soon departed for residence in a zen colony in Los Angeles. He surrendered the prizes I was still struggling hard to attain, a tenured professorship and a lovely house he'd built himself. In Zen, he hoped to attain oneness with the eternal essence of life, of being. We'd talked about it often, a life beyond the slings and arrows of academe. I felt a similar longing in myself, but it was for me, as for the vast majority of us, not a calling matched by any courage or conviction. So, Soulé lifted his spiritual sail and departed, and I was left with still more years of arguing the statistics of community assembly with the mafia from Tallahassee.

In its early phases of development the science of conservation biology suffered from reductionism. Extinction, both its prediction and the strategy for its avoidance, was a central theme. The difficulty was that the problem of extinction was attacked unidimensionally from various disciplinary perspectives—population genetics, island biogeographic theory, stochastic population dynamics. Thus we got disciplinary answers. Based on models of demographic stochasticity (MacArthur & Wilson 1967), 10 animals were needed to make a population safe from random birth and death fluctuations. Papers by Ian Franklin and Michael Soulé in the 1980 Soulé and Wilcox conservation biology book indicated on the basis of empirical patterns of population genetics that 50 animals were needed in the short run, 500 in the long run. Island biogeographic theory also gave guidance for strategy; for example, a single large reserve is better than several small reserves (Diamond 1975).

In the audience in 1978, I viewed the papers of the conference as interesting but not as revolutionary, not the start of anything. In effect, there was an applied side to these various disciplines. They actually spoke to something important. Good science in any of these areas would lead to good conservation biology. It was a comforting thought: our research as currently performed was of value. We should carry on.

And it was this that seemed to be Soulé's parting message to his stay-behind academic colleagues: our scientific work is important. Yet for Soulé the answer lay outside of academe. He quit. He cut his ties completely. He left UCSD unconditionally: no life preserver such as a leave of absence. He even gave away his house. He approached Zen with an open heart and a free mind, with no ego ties or financial bonds. This new journey had started shortly after I arrived to join him in the very molecularly oriented biology department at UCSD. He had taken a sabbatical to Australia. Among other things, he and Sir Otto Frankel started a collaboration that led to their 1981 book, *Conservation and Evolution*. Once he had started thinking about extinction threats and the fragility of life, Michael had what is termed The Ocean Experience. I gather that it's a special feeling of oneness with life. This got him reading and thinking. One track led toward oriental philosophy and to Zen Buddhism. He knew he had to follow it further, to explore its meaning for him more deeply. The international conference and the book on conservation biology were to be his swan song. His life was to be given over to Zen.

But other vital forces remained active and wrestled for place in his psyche. His 1980 book with Wilcox was a big success. And he found his rational faculties too strong to surrender fully to the mystical depths of Zen. He profited, but he returned. Back in San Diego, I could offer him no more than friendship and some assignable square feet in my lab. His colleagues could not be induced to return to him the position he had earlier earned. Soon, however, he had a number of our committed students working with him on various projects. His research horizons were widening. He began to fight his way back into the academic world.

Having read the 1980 volume by Soulé and Wilcox, Hal Salwasser of the USFS asked Soulé to organize a small workshop in 1982 to consider the issue of the minimum viable population (MVP). The 1976 National Forest Management Act contains a line in the second paragraph of the first page saying that "each forest superintendent shall maintain minimum viable populations of all vertebrate species." Under this legal mandate, how was his agency to deal with the Northern Spotted Owl, which was present in the National Forests of Oregon and Washington? Soulé asked me, Daniel Goodman, and Jim Brown to represent the academic side. Salwasser invited Mark Shaffer, Steve Mealy, and Fred Sampson to represent agency science.

The initial efforts toward a spotted owl MVP centered on the population genetics-based Magic Number 500. I was uncomfortable with this. My intuition suggested that fragmentation was the key factor endangering Northern Spotted Owls, but there was no Magic Number for fragmentation. Further, Soulé himself clearly saw the MVP problem as multidimensional. He had not asked four geneticists to attend the workshop; rather, he had asked a demographer (Goodman), a community ecologist (Brown), and an island biogeographer (myself) to join himself (a geneticist) to consider this problem from various vantage points.

Still, 500 was a nice number for managing Spotted Owls. With a "correction factor" between the effective population size N_e, and the census population size, N, of 4, there would be a requirement for 2000 Spotted Owls, with each pair requiring 2000 acres in its territory. The actual number of Northern Spotted Owls was then estimated as being close to 2000. Thus, scientifically to adhere to its mandated responsibilities, it appeared that the USFS had very soon to stop logging old-growth Douglas fir, the required habitat for Northern Spotted Owls.

The bristles on the back of fruit flies, from which the Magic 500 derived, led with careful logic and mathematics to the protection of 2 million acres of old-growth Douglas fir. Had ever the nonmedical explorations of genetics led to something of such economic immensity?

My eyes were opened at this 1982 meeting. Despite our initial flirtation with population genetics and 500, the question of MVP was clearly multidimensional and synthetic. It involved multiple selections from the full menu of population biology knowledge and expertise. MVP needed to be based both on good data and on comprehensive, realistic models. I believed I had the diversity of background and the computer modeling skills to attack MVP. I became a conservation biologist there and then.

The question of the parrots also presented itself to us in 1982. Although it had been exhilarating to imagine ourselves halting logging throughout the ancient forests of Oregon and Washington lest a long-lived bird population drop below 2000, it was a bit of a logical strain to attempt to say that 48 individuals of a different long-lived bird species was not cause for despair. We needed a common treatment and methodology for both cases. This was the spur that led us to formulate the approach we dubbed PVA.

The governmental (initially within the USFS) and policy response to our initial analysis of the Northern Spotted Owl was, of course, for more study. Salwasser funded additional meetings for Soulé and others to organize. One, in Michigan in 1984, led to Soulé's 1987 book, *Viable Populations for Conservation*, which better explored the constituent pieces of PVA. Soulé and I continued to work closely, to interact on a wide range of topics and projects, and—through theory, basic science, and case studies—we and others have added a body of work that guides our now more sophisticated approaches to species viability.

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