



Reflections on Michael Soulé, a visionary for conservation biology

On 17 June 2020, the field of conservation biology lost one of its founders. Michael Ellman Soulé died at the age of 84 in Colorado. During a long and productive career, Michael published 10 books and over 170 scientific articles, on topics spanning biology, philosophy, ethics, and of course conservation biology. Widely recognized for his contributions, Michael was a fellow of the American Association for the Advancement of Science and the American Academy of Arts and Sciences and recipient of a Guggenheim Fellowship, the Archie Carr Medal, the National Wildlife Federation's National Conservation Achievement Award for Science, the Conservation Medal from the Zoological Society of San Diego, and the E.O. Wilson Biodiversity Technology Pioneer Award. He was also recognized by Audubon Magazine as one of the 100 Champions of Conservation of the 20th Century. But he would probably claim as his proudest achievement his role in cofounding and serving as the first president of the Society for Conservation Biology (SCB).

Michael was born in 1938 in San Diego, California. His playground and first classroom were the arid chaparral canyons that define the area. Michael completed his undergraduate degree in 1959 at San Diego State University and his PhD in 1964 at Stanford University under Paul Ehrlich. In 1979, as a productive professor in the Ecology and Evolutionary Biology Department at the University of California San Diego, Michael quit in dismay at what he saw happening to nature, including urban development around his beloved canyons. He pursued Buddhism, which guided him throughout his life, and was the director of the Kudoba Institute for the Study of Buddhism in Los Angeles for 5 years.

In 1984, Michael returned to academia as a professor at the University of Michigan. That decade, his publication of four books and a series of key papers on conservation biology firmly defined the ambition of the new field and cemented his legacy as a visionary of the discipline.

His final years in academia starting in 1989 were as professor and Chair of the Environmental Studies Department at the University of California Santa Cruz. Michael advised two cohorts of graduate students there including the three of us, Gerard Zegers, Kelly Moran, and others. Evening graduate seminars at his home ran late into the night, with sofa and floor space filled with stu-

dents. He took us on trips south of the border to Baja to explore and survey the islands in the Sea of Cortez. Evenings were dedicated to reading sometimes mind-numbing philosophical texts. Michael's mentorship was transformative, exposing us to new ways of seeing the world.

After Michael retired in 1994 to western Colorado he traveled, river rafted, built a straw bale house, tried hunting, gave invited talks, and wrote. He worked on an unfinished manuscript describing conservation as an ethical pursuit, defined by a moral dilemma originating from the evolution of human sin and selfishness. It was a big idea, and as is often the case with transformative leaps, it evaded him in the end.

In the memorials that follow, colleagues and friends provide personal stories, spanning Michael's entire career, that reveal his impact as a scientist and a human being. One of our own is the time Michael made dollars rain from the sky. It happened in 2000, at the SCB Annual meeting in Missoula, Montana. Michael, a scientist with an activist heart, gave a stirring speech to a packed house advocating for SCB to establish a policy-focused office in Washington, D.C. in order to directly translate the best science into conservation decision making. As his speech built steam, Michael asked everyone who agreed with his position to initiate a DC SCB office to reach into their pockets and pass a dollar bill to the aisle for collection by the three of us. As we ran up and down the aisle, more bills started fluttering down on the crowd, flung by people in the balconies. It was truly a magical moment. Everyone was on their feet roaring their approval, bills floating like confetti while Michael stood immaculate on stage, softly lit, with a hint of a smile, an aged lion back on familiar ground.

Michael intensely felt the burden he placed on his students. He taught us the truth about loss and grieving for nature, for life on Earth, but without allowing despondency to deplete our aspiration. His commitment to the next generation of students, and the generation after that, was evident when he dedicated his classic *Conservation Biology* book (Soulé 1986) to "the students who will come after, who will witness the worst and accomplish the most."

The three of us can trace our passion for conservation and the foundations of our careers directly to our years with Michael. Countless others would say the same.

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Anne and I first met Michael Soulé in the early fall of 1959, when we all arrived at Stanford's Department of Biological Sciences, me as a beginning assistant professor, and Michael as a newly admitted grad student. He, along with Harry Recher, became my first grad students, and lifetime friends and colleagues. Michael showed his independence and humor from the very start. I had invited Ernst Mayr to give a seminar, and near the end of his talk he said, "I always instruct my grad students to tell me if they think I'm mistaken." Michael then quipped "does that go for grad students at other universities, too?" Ernst laughed, but Vic Twitty, our Department Chair, sitting next to me thought it a terrible insult to a distinguished visitor and whispered I should get rid of Michael. Fortunately Ernst was fine, I disagreed with Vic, and Michael went on to be a leading scientist and to found the field of conservation biology.

When Michael and his wife Jan were living in Africa on the outskirts of Blantyre, where Michael was helping found the first university in Malawi, he organized and ran a Safari for Jan, Anne and me, and Lisa, our then 10 year-old daughter. In then-Portuguese East Africa, we skirted the war between Salazar's Portuguese dictatorship and the Frelimo, who were then battling to free the country. We saw villages burning, but most frightening was Michael speeding along roads that consisted of two approximately 6-inch-wide paved strips, resulting in spectacular games of chicken when we met vehicles traveling in the opposing direction.

In southern Rhodesia (now Zimbabwe), we all committed the capital crime of criticizing Ian Smith's government, but because of our skin color we did not end up on death row. When we were returned to our motel in Salisbury (now Harare) one night by the black law pro-

fessor and his attorney wife with whom we had dined, the motel owner intercepted us and explained how dangerous it had been for us because "they are just out of the trees." It is sad that we have lost Michael just as he could have helped to battle racism here at home as he had in Africa.

Paul R. Ehrlich

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Michael Soulé was the first graduate student I met at a 1962 welcoming party for new students at Stanford. He was several years into his PhD and was friendly and encouraging, with kind, penetrating eyes as we discussed our interests and backgrounds. We became good friends.

With his encouragement, I spent two summer months in the Colorado Rockies and accompanied him on several field excursions. We explored, collected butterflies and lizards, took photos, and talked along the way. Michael had broad interests in evolution, and he felt confined by the specialization of his dissertation in phenetics. However, his passion for nature was contagious and he decried its profligate destruction.

He was a charismatic visionary throughout his life. As the campus leader of Vietnam War protests, he moved students to political action with powerful rhetoric. I joked that he owed his dating success to these skills. At the same time, he led smaller groups in quiet exploration of the hidden powers of the mind through meditation and ultimately Buddhism. With others he founded the crisis science of conservation biology and the eponymous society and was its first president.

Michael was a teacher and mentor, insistent on the inherent value of nature and skeptical of the trend to treat wildlands as gardens and to value them as a commodity. He taught that nature is too precious and central to our physical and mental survival to be monetized, subdivided, and privatized. He challenged us to find a way to live within a connected web of wild, untrammelled nature. This is a fitting rallying cry to carry his work forward.

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Michael Soulé was living at the Zen Center of Los Angeles when I first met him in the early 1980s. At that time, we were both very interested in the relationship

between multiple locus heterozygosity and fluctuating asymmetry as a measure of fitness (Soulé 1979; Leary et al. 1983). Michael invited my student Robb Leary and myself to present a paper on heterozygosity and fitness at the Second Conference on Conservation Biology at the University of Michigan in 1985 (Allendorf & Leary 1986).

Michael's enthusiasm for the importance of this topic in conservation inspired us to continue this work. Those early efforts continue today in genomic studies exploring the relationship between multiple locus heterozygosity, inbreeding, and fitness. For example, my former student Marty Kardos recently examined the relationship between inbreeding and multiple locus heterozygosity in Scandinavian grey wolves with 10,688,886 single nucleotide polymorphism loci (Kardos et al. 2018). In comparison, we examined just 13 polymorphic protein coding loci in our 1983 paper.

My primary memories of my discussions with Michael over the years focused more on Zen than on biology. I was new to Buddhism when we first met, and Michael served as a Zen Master of sorts. I still remember Michael asking me to explore the concepts of self and emptiness during meditation.

Michael's efforts over the last 50 years of his life are reflected in the following traditional Zen vow: "The many beings are numberless; I vow to save them all."

Michael never stopped trying.

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Michael Soulé and I both became interested in inbreeding in small populations in the late 1970s. He was familiar with population genetics, whereas I was not when I discovered that inbreeding was a problem in ungulates at the Smithsonian's National Zoo in 1976 (Ralls 1997). And neither was Jon Ballou, then my assistant.

Seeking advice, I visited Michael, then at the Zen Center of Los Angeles. He was in a yellow robe, helping to prepare the vegetarian lunch for the group. But when I asked him about some population biology question that bothered me, he wiped his hands on his apron, took me to his office where he had a blackboard, grabbed some chalk, and immediately reverted to professorial mode, going through the math that had eluded me.

In 1984, Jon and I organized a workshop to develop consensus on genetic management of captive populations. We invited about 30 leading experts and divided them into groups. Michael's group advised that the principle goal of captive breeding should be maintaining 90% of the genetic variation in the source population for 200 years (Soulé et al. 1986). This goal is now used in captive breeding programs at zoos globally, although the time is often shortened to 100 years for practicality.

Michael and I were among those recommending that the U.S. Fish and Wildlife Service bring the last surviving California Condors into captivity in 1987. In 1990, he advised the agency that I should be the population's genetic manager. At first there were only 27 birds, and I was able to do this with colored pencils. Now that there are over 500 living birds and over 1,000 in the studbook, and management requires the computer program Jon developed. And, we are on track to achieve Michael's goal of preserving 90% of the genetic variation for 200 years.

In the late 1980s, I helped Michael found the Society for Conservation Biology. He told me: "Think about some prizes, we need to have lots of prizes, scientists spend so much time criticizing each other's work that we need to give them more positive recognition."

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My first correspondence with Michael Soulé was in 1982. I was an ecologist with the Ohio Natural Heritage Program and was already proudly calling myself a conservation biologist, having devoured Soulé and

Wilcox (1980) soon after it was published. In reading a subsequent book (Frankel & Soulé 1981), however, I was troubled by their warnings, based on theory, that habitat corridors could do more harm than good. Being involved in corridor conservation efforts, I brashly wrote Michael to point out that the corridors conservationists are trying to protect or restore are naturally present in the landscape and therefore unlikely to do harm. To my delight Michael wrote me back promptly, thanking me and saying he agreed. That was the kind of guy Michael was: humble, open-minded, and generous.

Years later, in 1991, Michael and I were among the cofounders of the Wildlands Project. I became the science director and Michael president. For years we argued vigorously about the mission and strategy of the organization. I favored comprehensive biodiversity conservation and restoration, whereas Michael thought we should concentrate on large carnivores and their needs for big reserves and connectivity. Finally, Michael suggested the two of us meet privately. We had dinner and several drinks, hashed it out, and emerged good friends again and in agreement. The ultimate result was the first published article on rewilding (Soulé & Noss 1998). Rewilding is now a global movement.

Would there be conservation biology without Michael Soulé? Maybe, but it would be less passionate, less complete. Michael had the intellect, charisma, sense of humor, and Zen attitude of commitment that would be difficult to replicate. He will be remembered as the leading visionary of our field.

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While reflecting on Michael Soulé's life, I went back and reread a few articles from the 1980s, when I first encountered him. It was a very different world. Conservation biology did not exist as a scientific discipline, and there was no journal or scientific society. In fact, some commentaries on Soulé's early work note with surprise that academic ecologists were becoming involved in conservation, then the domain of wildlife and natural resource

managers. Compare this to the situation today, and you will have some understanding of his impact. He founded our discipline and led and guided it through its formative years. I am proud to be one of the first members of the SCB, to have served on the board and as president, and to have seen the society grow, thrive, and ultimately mature into the establishment organisation that I do not think Michael ever quite came to terms with!

His influences are everywhere. Personally, I am indebted to him for his science and for his passion. His 1987 book, *Viable Populations for Conservation* (Soulé 1987), was my go-to guide when I was struggling to write species conservation plans in the 1980s and 1990s. It is still a great resource. Soulé's first chapter covers a lot of ground, most of which is sound advice even today. As I stumbled through my early efforts in conservation science, Michael Soulé was my guide. In 1992, I was lucky to be awarded a Pew Fellowship, which involved annual retreats with other fellows and the Pew Advisory Board. To my delight, this included Michael Soulé. I was in awe of this group of people, but he was always down-to-earth, entertaining, knowledgeable, and very kind as well. I learned much from him. He warned us repeatedly not to compromise in this, our crisis discipline. He will be hugely missed, but his legacy is enormous.

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I met Michael Soulé in 1988 at the Society for Conservation Biology's annual meeting. A year later, he moved to UC Santa Cruz as Director of the Environmental Studies Program, which at the time was floundering. Santa Cruz touted itself as an environmental campus, and Michael's charge was to save Environmental Studies. I watched in admiration as he pursued that mission with a bold and creative vision on the one hand and a masterful application of pressure and persuasion on the other. We became close friends. I grew to understand that he was gentle on the surface, but tough and uncompromising when it mattered.

Michael's and my professional relationship developed from a common interest in predators. We spent many an evening together with a bottle of wine, feasting on fish or game, and convincing one another that apex predators were essential for biodiversity conservation. We recognized that the simple persistence of a species was not enough. Michael's agenda for conservation thus

expanded from “demographic viability” (Soulé 1987) to “ecological effectiveness” (Soulé et al. 2003), a view that became the conceptual centerpiece of *Continental Conservation* (Soulé & Terborgh 1999), his last book.

Some may think Michael’s reverence for nature included an abhorrence of animal harvesting, but that was not the case at all. We both enjoyed the spoils of hunting and fishing and embraced the lifestyle as the right thing for any practicing omnivore to do. Michael was entirely comfortable slaying and eating the overabundant elk and deer on North American landscapes that had been stripped of their native predators. Although we lamented the dysfunctional nature of a world without predators, hunting wild ungulates in wild places had the beneficial consequences of putting meat on the table and nourishing our souls.

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Michael Soulé shaped my career and my approach to conservation biology in many ways. Michael hired me, fresh out of grad school, to join the Environmental Studies program at UCSC and then fostered my career there. I was lucky enough to interact with Michael in a range of contexts and to see how he so effectively promoted conservation science and conservation action. Among the most enduring lessons I absorbed from him was that we should not be afraid to make moral, as well as scientific, arguments for wild places and biodiversity. As he forcefully argued, most humans, even most environmentalists and conservationists, continue to prioritize the preservation or restoration of the rest of nature far below the desires or needs of humans, drastically limiting the scope of any possible conservation strategy. This calls on those of us who are biocentric, as Michael would say, to make explicit efforts to widen the moral compass of humanity beyond our own species. The other lesson of Michael’s that I think of most came from watching how he separated judgments of people from his arguments

with them. Michael was remarkable in his ability to make sharp judgments, hold vehement beliefs, and forcefully argue for them, while still being accepting and kind to the people he engaged with. This rare ability to not conflate judgments of a person’s worth with the worth of their analyses or opinions is, in my experience, exceedingly rare, and it gave Michael a calm energy and also optimism that it would serve many of us to emulate. Together with his scientific skills and insights, Michael’s broad perspective on the politics and underlying beliefs behind conservation and his personal ability to lead others allowed him to forge a path for conservation biology that the rest of us are still pursuing.

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I remember one incident, more than any other that made me appreciate Michael Soulé’s humanity as an individual and his genius as a communicator. We were both invited to give talks to the Second Brazilian Parks Congress, a major event held in Campo Grande, Mato Grosso that attracted 2000 attendees (imagine a conference on parks doing that here!). It was in November, 2000, at the fateful time of the U. S. election. I gave my talk first. It emphasized all the things Brazil was not doing that it could to conserve its almost unrivalled biodiversity. The tone was deservedly critical, but that is not what wins hearts and minds, if only because people do not feel ownership of policies enacted by politicians they did not help elect. Michael got it right. He talked from his heart on a personal level, saying how much he valued nature, how much it mattered to the quality of his life in so many ways, and how much pain it inflicted on him to bear witness to nature’s destruction. When he finished, there was hardly a dry eye in the hall. That was Michael. He could move strangers to tears with what he felt so deeply.

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I came to know Michael Soulé professionally and as a friend when he spent a few summers at Rocky Mountain Biological Laboratory (RMBL) with his sons in the 1980s. He was returning to where he met and eloped with his first wife in the 1960s. His interest in ecology led him to explore the role of pocket gophers in maintaining meadows (turns out they would rather starve than

eat aspen roots) and to initiate a long-term project on insect abundance, which I have continued since he left RMBL (a manuscript with Michael as a coauthor is now in review).

Michael encouraged me to retire to Paonia, a small town in rural southwestern Colorado (home to the highest-altitude wineries in the United States and the largest concentration of organic farms and orchards in the state), which he had made his home, and we took his advice. His home there at the time was a straw bale house he built with solar heating and small ponds where he enjoyed watching local amphibians. He found ways to use his scientific knowledge locally, such as serving on the local mosquito control board to encourage more biocontrol and less spraying, but he still continued international travel and speaking. I joined the weekly lunch group he and a few other friends had organized, which was often the venue for discussions of a philosophical nature.

A few years ago he asked for opinions about whether he should protest the local coal mines by lying down on the railroad tracks to stop a coal train.

Michael's avocations also defined him. He enjoyed international folk dancing and contra dancing for at least 50 years and was a regular participant in the music and dance scene in Paonia. He loved being on rivers and joined us on some long river trips, including a 16-day Grand Canyon trip when he rowed his own raft and shocked another participant when he picked up and kissed a toad.

Michael was happy that a pack of wolves arrived in Colorado recently and hoped he would see the return of grizzly bears. If one does show up soon, I will have to wonder whether it is Michael in his next incarnation.

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