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IJEE Soapbox:

A meditation on life, death, and meaning

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We live in a wounded world. Some wounds are personal, intimately entwined with one's very being. Others are not personal, but communal, in an expansive sense of the word. Part of living a human life is the accumulation of wounds within oneself, physical and psychic, and trying one's best if not always to heal, at least to cope with them. Even the best of lives, far from the travesties of tyrants, thugs, and terrorists which so fill the news, knows sadness and grief. Why? Because all of us are mortal, and so we ourselves, and everyone we care for, will disappear, someday, somewhere, somehow. As a Confederate Episcopal bishop noted in 1862 during the American Civil War, "We all have our dead – we all have our graves" (quoted in Faust 2008, p. xi), and we bear through our lives the wounds of such losses. I still miss relatives such as my sweet and perceptive great-aunt Ethel Mills, who died in her 80s when I was in my early 20s. This sadness is sharpened, almost unmeasurably, when misfortune unexpectedly snatches life from someone in our ambit, long before the normal course of a human life is expected to end. Much of the musings of philosophers and the rituals and texts of religious traditions can be viewed as attempts to deal with such finitude.

The famed philosopher and polymath Bertrand Russell, who lived to 97, ended his great essay "How to Grow Old" (Russell 1956, p. 51) with the following eloquently expressed thought: "The best way to overcome it [a fear of death] is to make your interests gradually wider and more impersonal … [so that] your life becomes increasingly merged in the universal life. An individual human existence should be like a river: small at first, narrowly contained within its banks, and rushing passionately past rocks and over waterfalls. Gradually the river grows wider, the banks recede, the waters flow more quietly, and in the end, without any visible break, they become merged in the sea, and painlessly lose their individual being. The man in his old age, who can see his life in this way, will not suffer from the fear of death, since the thing he cares for will continue. … I should wish to die while still at work, knowing that others will carry on what I can no longer do." A related line of thought has been developed recently by the philosopher Samuel Scheffler in his *Death and the Afterlife* (2013), who argues that much of the meaning in a human life comes from the fact that we believe in a kind of secular "collective afterlife" (a phrase of Kolodny, in Scheffler & Kolodny 2013, p. 5), comprised of all those human beings who will live on past our own existence. Scheffler states (p. 30) that it matters "to us to have other people we care about live on after we die, and it also matters to us to be remembered, at least for a while." He goes on to note that one way we preserve values into the future – values that govern our current lives – is to engage in group-based traditions that support those values, thus in a sense extending beyond ourselves into future generations. By participating in religious and cultural traditions, the functioning of democracy via political parties and other forms of social engagement, fostering family rituals, and so forth, one helps to preserve whatever one values in life (see also Scheffler 2010) in the ongoing river of life that continues after one's death.

I think one can distinguish three nested sets in the "collective afterlife" (the structure of engagement with our conspecifics, past, present, and future, is more complex than this, but using this structure as a scaffolding will lead to where I am going later in this essay). There are, on the one hand, those humans whom we have (or will have) significantly, causally influenced in various direct ways (one would hope, positively). These would include family, friends, lovers, neighbors, students, and teammates, among others. Then, there are all those humans we have indirect impacts on, either percolating through intertwined networks of direct interactions, or through durable cultural and physical artifacts. A junior high teacher could, for instance, have an indirect influence in her community resonating well beyond the students she taught, and across multiple generations, through how those scruffy students integrated her teachings into their own behavior in private and public arenas through their lives. For scholars and scientists, this indirect influence might be through their writings, for generations to come (in this essay alone, here in 2016, I have already cited Bertrand Russell, who died in 1970). Humans talk, and read, and watch, and learn from

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Robert D. Holt is our invited ***IJEE Soapbox*** essayist. Bob is a professor of biology and Arthur R. Marshall, Jr., Chair in Ecological Studies at the University of Florida, and is one of the foremost theoreticians in ecology and evolutionary biology. His research focuses on theoretical and conceptual issues at the population and community levels of ecological organization and on linking ecology with evolutionary biology. Bob is best known for his pioneering work on apparent competition, multispecies interactions in food webs (community modules) in time and space, and the evolution of niche conservatism.
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each other, and such social learning arguably underlies essentially all the evolution of cultures (Boyd & Richerson 2005). Hodgson and Knudsen (2010) suggest that habits and routines, including traditions, viewed as learned dispositions to behave in a certain way that are passed on from one individual to another, are the replicators underlying much of cultural evolution.

Given that we are all the products of an evolutionary process unfolding over almost countless years, it makes sense that a major part of the grounding of the values that govern behavioral choices in our individual lives has to do with the presumed existence of humans in the future, including in particular humans whose lives will be influenced by what we say, do, and believe. We, after all, descend from individuals who must have been governed by such forward-looking values, themselves. By paying attention to the future, belief systems can in effect bootstrap themselves through time, and as repositories of such beliefs, and because we can act as agents to foster comparable attitudes in others, we ourselves in a sense replicate part of ourselves (our beliefs and values) into future generations. Knowing this helps at least a little in assuaging the wounds we all carry from the deaths of those for whom we care.

Beyond causal chains linking us in the present to future generations indirectly via learning, we also can leave deliberate physical imprints on the world (i.e., human niche construction, in a literal sense; Odling-Smee et al. [2003]). For philanthropists, this might be via establishing hospitals or schools or museums. For an engineer, this might be through designing a sound bridge or subway system. For an academic, this might be putting together a set of publications on a general theme, which collectively might have more impact than when each paper is published separately. Until very recently, these compilations would have been bound volumes in a library; increasingly, these exist in electronic form only.

I did not have the honor of knowing Dr Keren Embar personally, but I am moved by the compilation of research publications brought together in this volume to honor her memory and contributions to science. I have read with admiration papers she authored on game-theoretic problems in predator–prey interactions, both in other venues (e.g., Embar et al. 2011, 2014), and in this issue (e.g., Kotler et al. 2016). So, I am in that set of humans already indirectly influenced by her all-too-short life. And this cultural artifact, this collection of intertwined papers, will project into the future, to allow many more humans to be influenced in their own lives by Dr Keren Embar.

There is a third, outer set in the "collective afterlife," namely humans (or their artifacts) whom we neither directly nor indirectly causally affect, to any measurable extent, but whose continued existence, or the contemplation thereof, in some way helps imbue our own lives with value. For instance, my heart thrilled when I read that the Malian archivist and historian Abdal Haidara in Timbuktu in 2012 saved hundreds of thousands of medieval Islamic manuscripts from the ravages of occupying Al Qaeda militants, by smuggling these precious documents to safe havens further south (Hammer 2016). To my eyes, those texts are part of the heritage of our entire species. They are not obviously part of the life of any set of people over whose lives I have a causal influence, at present or in the future, and they are not clearly engaged in the traditions that have been part of my life, but nonetheless it matters that this trove of manuscripts are out there and can influence the lives of future people in other cultures and traditions, well outside my own. By contrast, the destruction of the Temple of Bel in Palmyra, Syria, by brutal extremists (Barnard & Saad 2015) is heartbreaking, and a terrible loss, a degradation in the world – a wound to our collective humanity, now and in the future. Such wounds are beyond the personal, a kind of harm inflicted on the metaperson of our species.

I can of course indirectly have a (rather minor) influence on happens in Timbuktu, for instance by voting for US senators or representatives likely to support sending UN peacekeepers there. But the magnitude or even existence of such an attenuated (if it even exists) causal chain of influence does not obviously affect the moral value I ascribe to the continued existence of that precious horde of medieval Islamic manuscripts. Maybe one should think not about actual causality, but potential causality. Were I to receive a reliable solicitation in the mail, pleading for funds to help sustain the continued preservation of these manuscripts from Timbuktu, I might well respond with a check. But this probably shows that I likely had a prior valuation of those manuscripts, prior to such a solicitation materializing in my mailbox. So the fact that I value the perpetuation of that cultural legacy does not really depend on whether or not I have any causal influence on its future fate.

I would like to suggest that one might extend these ideas about how the values we cherish in our lives in some fashion embody the presumption that we will impact future human lives. In particular, an argument could be sketched along these lines that encompasses an even broader swathe of living reality, namely the manifold diversity of species with which we share this planet.

Let me take what seems to be a digression, for a moment. The subtle phenotypes wrought by adaptive evolution never cease to amaze. Consider the elegant empirical study by Kotler et al. (2016, this issue) on the lack of convergence in behavior between morphologically convergent rodents – one from the American Southwest, the other from the Negev Desert of Israel – carried out with "common garden" experiments. Such studies help to shed light on how unique traits that arise in evolutionary history, in combination with adaptively labile behaviors, can help determine large-scale variation in community structure across regions with comparable climates. Theoretical studies such as the one by Brown et al. (2016, this issue) complement such empirical studies, highlighting aspects of dynamical systems that are missed in standard approaches to ecological forecasting, with ramifying effects on the effectiveness of model projections. In particular, Brown et al. (2016) show that incorporating adaptive behaviors into predator–prey models can stabilize otherwise-unstable interactions. So adaptive reasoning about what organisms do is I think an essential arena of thought, in both basic science and applied disciplines.

It is important to remember that adaptations are always defined in relationship to a particular range of environmental conditions, and if organisms are pushed outside the environments they experienced in their evolutionary history, maladaptation is to be expected, and even extinction. Evolutionary biology and ecology can be used to develop a theory of maladaptation (Crespi 2000). One aspect of the theory of maladaptation that has been receiving increasing attention is the theme of evolutionary rescue (Gomulkiewicz & Holt 1995; Gonzalez et al. 2013) – the phenomenon where in a changed environment a population is initially declining toward extinction, but natural selection then acts sufficiently rapidly to increase mean fitness and permit that population to rebound. Phenotypic plasticity can facilitate persistence (Lande 2009; Merila & Hendry 2014), as well as can factors such as abundant genetic variation and more gradual environmental change. Yet such rescue must often fail, as witnessed by the current rate of species extinctions, orders of magnitude higher than background extinction rates (Kolbert 2014). These current extinctions come on top of the historic wave of extinctions of megafauna coincident with the expansion of *Homo sapiens* around the world. (Maybe we should re-name ourselves *Homo eversor*, where the latter word is Latin for "exterminator.") Joel Berger (2008) has argued that many extinctions precipitated by the invasion of humans surely involved the absence of fear by large mammals confronted for the first time by a predator as, well, "different" as our species is from the other taxa they may have justifiably feared in their evolutionary histories.

Environments that radically change, but in ways not readily perceived by taxa, are particularly insidious, in terms of species survival. Vultures in much of the Old World, in particular the Indian subcontinent since the 1990s and now Africa, are precipitously declining toward extinction (Ogada et al. 2015). The principal cause in Asia is the incidental poisoning of vultures by diclofenace, a non-steroidal, anti-inflammatory drug given to cattle to boost their overall health – and a substance which is highly fatal to vultures which consume dead cattle (Doherty 2013). Nothing in their evolutionary history would have prepared these vultures for this shift in the chemistry of the carcasses they scavenge. In Africa, the story is more complicated (Ogada et al. 2015), but pesticides and deliberate poisoning (by poachers) again appear to be dominant causes. Across the globe, another wave of extinctions of terrestrial megafauna is underway (Ripple et al. 2016), and many drivers of extinction have to do with causal factors well outside the scope of the evolutionary history of the species at risk. More wounds, all wounds that will never heal, every species driven to extinction by humans is like a wound on the body of the planet.

Many of these species plummeting toward their doom do potentially (or actually) provide benefits to humans of one sort or another, and saving them for future generations makes good sense, in terms of how we value their continued existence. Vultures obviously can provide efficient garbage disposal services, but they can also provide more subtle benefits. Ogada et al. (2015) describe how the absence of vultures in the Indian subcontinent has led to a surge in feral dog numbers, which in turn has greatly boosted the risk of rabies to humans. Ripple et al. (2016) note more broadly how mammalian megafaunal species can have dramatic effects on their ecosystems, for instance, via top-down trophic cascades, or massive ecological engineering effects on landscapes, many of which have consequences for human activities. All these effects are important to understand, and document, and build into management decisions, whenever possible. One important line of argument for conservation is thus utilitarian, in terms of retaining something that might be valuable in various pragmatic ways for our descendants.

But hold on… I was horrified at the news of the destruction of the Temple of Bel, not in particular because I hoped to visit there myself (a potential utilitarian benefit because of the pleasure I might have gotten from the site) but because this malevolent act so cheats future generations (including many humans far outside my extended causal network) of significant potential intellectual and aesthetic experiences. In this journal a few years ago, I mused that every species has a unique story to tell, and should be worth preserving, for that fact alone (Holt 2009). McCord, in *The Value of Species* (2012, p. 9), argues that "… Individual species are phenomena in this world of such intellectual moment – phenomena so interesting in their own right – that this alone gives them a value meriting human embrace." So one argument for conservation, tied to the line of thought suggested by Scheffer (2013), is simply that we should preserve as many species as we possibly can, so that future generations can enjoy the intellectual pleasure that comes from uncovering the stories each can tell.

And understanding species and their implicit stories really requires one to understand the tangible environments in which they evolved. Many of those environments are extraordinary places to visit, providing rich intellectual and aesthetic rewards in their own right (as in the travel tales recounted in Dinerstein [2013]). One can certainly get a thrill seeing a lion in the Bronx Zoo, but this pales compared to the sight of a pride of lions loping across the Serengeti. An intellectual appreciation of species requires not just persistence of that lineage into the future, but somehow retaining a reasonable facsimile of the environment in which that species has lived.

To return to Scheffler's conjecture that our expectation of a "collective afterlife" underlies many of the values we have, given how poorly understood the biota of the earth is (particularly when one considers small-bodied organisms, or denizens of habitats hard to reach, such as the deep sea), most of these stories will be "read" by future generations – if at all. But if the current mass extinction proceeds apace (Wilson 2016), it will be as if Al Qaeda had indeed set fire to all those medieval manuscripts from Timbuktu – once gone, no one will be able to read those stories.

I personally believe that other species do have intrinsic value, beyond utilitarian concerns, the desire to retain species across the phylogenetic spread of life for the intellectual delectation of future generations of humans, or even the need of humans to connect with other living

things due to the particular circumstances of our shared evolutionary history (the biophilia hypothesis of Wilson 1984). This belief concords with the views of some environmentalists (e.g., Ehrenfeld 1972; Norton 2003). But articulating where such values are grounded is difficult in the absence of some kind of engagement in the future with humankind.

I have in my own life experienced the wounding of the earth by the extinctions of several vertebrate species, without quite grasping what was going on at the time. Back in 1972, I spent a summer with a friend, Sam Test, in Mesoamerica, including several days camping around the magnificent Lago de Atitlàn in the highlands of Guatemala. Along with soaking up the stunning scenery and rich local culture, we were in quest of the flightless Atitlan Grebe, *Podilymbus gigas*, a large-bodied relative of the more widespread and familiar, smaller and flying, Pied-billed Grebe *Podilymbus podiceps*. This flightless bird was known from only this one lake. With the help of a kindly priest (Father Stanley Rother, later murdered by the brutal military government reigning in Guatamela in those years), we were able to get to a rather inhospitable stretch of shore where the endemic grebe was reputed to nest in a refuge, and we managed to see a few on the water. How painfully sad it was for me to learn years later that the species was already in decline at the time of our visit, due to introduction of smallmouth bass *Micropterus dolomieu* and largemouth bass *Micropterus salmoides* (which both competed with the grebes for food, and fed on their chicks – a somber instance of the conservation implications of intraguild predation, Holt and Polis [1997]). The last Atitlan Grebes were seen in 1989, and given that there is basically no place to hide in this montane lake, they are surely gone forever. There are so very many questions one might like to ask about this species, questions that will never have an answer, chapters of its story that are never to be read. Did Atitlan Grebes have reduced metabolic rates, comparable to what is observed in many island taxa (McNab 2012), and for comparable reasons? Were there correlated changes in life history traits, or social behavior, emerging from this bird's restricted dispersal abilities? We will never, ever, know.

Sadly, I have also encountered two other vertebrate species that are also very likely extinct. In December 1979, along with my wife and some graduate students from the University of Kansas, I made an expedition to the Yucatan, including a foray to the island of Cozumel, which has several species of endemic birds. One morning, I caught a glimpse of one, the Cozumel Thrasher (*Toxostatum guttatum*). It resembles its mainland relatives, so other than enjoying the fact that I had seen another species to add to my life list, I did not pay much attention to it. I do recall thinking that unlike some island species, its population did not seem all that high (that one individual on the one occasion was the only one I saw). But now, the bird has seemingly not been seen for about a decade, according to Humberto Berlanga of CONABIO (personal communication). The reason for its disappearance is mysterious; some blame an introduced predator, the boa constrictor, a snake which when young definitely feeds on birds. No one really knows. Another wound in the body of life.

The other story of in-the-face species extinction I stumbled across (almost literally) in June 1980. I was at Monteverde, Costa Rica, for a few days, poking around before joining an Organization for Tropical Studies course in which I was teaching. One evening, I somewhat foolishly decided to take a trail by myself through the cloud forest along the Brillante Ridge, in the hope of coming across calling owls, despite it being chilly and damp. After I had gone some distance in the dark, it started raining, hard, really hard (ergo, no owls on offer), and I had to turn around and gingerly walk back to my base. Slipping and sliding over the slick, muddy, moss-clad trail, constantly looking at my feet so as not to trip and doubtless fall off the ridge, just before I was about to step into a puddle of uncertain depth, looking down I saw in the beam of my headlamp a squirming mass of – gold. I managed to awkwardly adjust my stride to straddle the trail rather than squish whatever was in view. After wiping off my glasses so I could really see what was in front of me, there they were – a group of Golden Toads, *Incilius periglenes*, going enthusiastically at it. I knew rather little about this species, but learned later (Crump 2000) that after spending the months of the dry season in burrows underground, when the heavy rains hit, the toads would emerge and engage in explosive sex, with males amplexing with any golden thing they could get their lustful limbs onto. I only watched them that evening for a few moments, before sloshing away homeward, but now I wish I had spent the rest of the evening simply poring over that puddle with its golden trove and savoring its display of life – because now, they are all gone. The last Golden Toad, a doubtless desperately lonely male, was seen in May 1989 (Crump 2000). The reason this beautiful species disappeared from its montane realm is still subject to debate, but climate change combined with a fungal pathogen (the chytrid that is so devastating amphibians around the globe) surely did them in. Wound, after wound, after wound. How utterly sad.

This essay has been so rather bleak, let me end on a somewhat more hopeful note, and think about the joy and fun and cheerfulness that Burt Kotler (2016, this issue) notes in his reminiscence of Dr Keren Ember as defining features of her persona. There is a Chasidic saying from the eighteenth century that I have taped on my office wall: "Just as the hand, held before the eye, can hide the tallest mountain, so the routine of everyday life can keep us from seeing the vast radiance and the secret wonders that fill the world." (Source: unknown). Even with all its tragedies and losses, the capacity for humans to learn, and play, and explore, and simply soak up the comforts of companionship and the beauty of life, helps the pain of wounds to heal, and life to go on. We can take joy in the fact that conservation successes are occurring all over the world. Bill Laurance has just published an online essay (http://biographic.com/posts/sto/no-lost-cause), outlining a number of major conservation victories. When I was a young birder, back in the 1960s, the Bald Eagle (*Haliaeetus leucocephalus*) and Osprey (*Pandion haliaetus*) were both

incredibly rare in much of the United States. Now, in many places one can see them every day. The Mauritius Kestrel (*Falco punctatus*) had declined to a population of four (4!) individuals at one point, but a combination of targeted breeding and habitat management has brought this species back from the brink of all-but-certain extinction. Michael Rosenzweig (Keren Ember's academic grandfather, transmitted through Burt Kotler, his student) coined the term "reconciliation ecology" (Rosenzweig 2003) to encompass the many ways humans are modifying their environments to permit cohabitation with a broad array of species. There is room for hope. For hope in conservation to be realistic, conservation efforts need to be based on a deep scientific understanding of organisms and their environments. Thus, addressing the subtleties of adaptations, and the intertwined interactions of species responding adaptively to each other (as explored so effectively by Karen Ember, and as represented in these papers gathered in tribute to her), should be at the heart of our collective efforts to reconcile our presence on the earth with the continued existence of so many of the other species that are our companions on this ark.

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