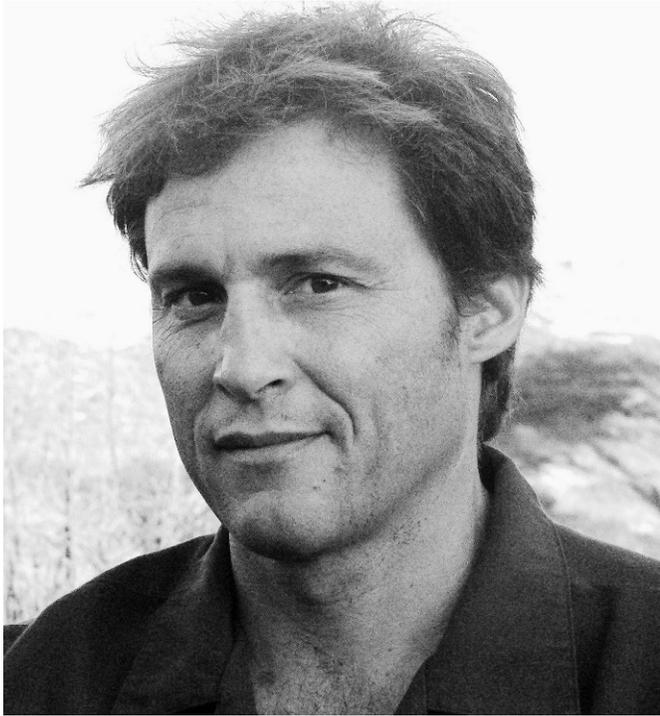


## ACCEPTANCE OF THE 2009 HENRY BALDWIN WARD MEDAL: THE ACCIDENTAL PARASITOLOGIST

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Members of the Society, President Conn, colleagues, friends, and particularly students, the Ward Medal recipient, from Clarke Read onward, traditionally recounts how their career was shaped. A decade ago, in a crumbling Kona hotel, the ASP's own tattooed lady, Janine Caira, opened her Ward Medal address with: "To all future Ward Medalists, many of whom I trust are sitting in the audience out there today, I say: savor the moment! You have no idea how much easier it is to be sitting out there where you are than standing up here where I am" (Caira 1998). I certainly didn't imagine that Janine was delivering her advice to me and it is presumptuous to imagine my story is a template for shaping a career. As the title of my talk indicates, it was an accident.

I spent my childhood in loving comfort. My younger sister Tina and I were raised in the Los Angeles suburb of La Cañada. My father Lanny worked for NASA at the Jet Propulsion Laboratory as an aeronautical engineer and my mother Libby was an author and entrepreneur. We lived on the "poor" side of a wealthy community, with only 1 Mercedes in the driveway (and a second-hand one at that). With the support of my parents and like-minded neighbor kids, I gravitated early toward biology with a fondness for zoos, aquaria, natural history museums, and field guides. I spent much of my free time drawing animals. Otherwise, my father drove me to various youth sports activities that he often volunteered to coach.

Summer vacation provided my first field experiences. My grandparents owned vacation rentals on the Balboa Peninsula in Newport Beach. Every summer, my parents would take us and various cousins to stay in the upstairs unit, while managing the downstairs rentals. A block to the west was the sandy beach, a block to the east was Newport Bay, a block to the north was the library, and a block to the south was an adult movie theater. By spending the summers body surfing, sailing, fishing, and beach combing, I familiarized myself with the sand crabs on the beach, mackerel caught from the pier, and mussels and crabs on the pilings, deciding at 13 to become a marine biologist. Without a television, I read excessively. Unknown to me, at the other end of Newport Bay, Walter Martin, a parasitologist at the University of Southern California (USC), was describing the larval trematode community of the California Horn Snail, *Cerithidea californica*; his efforts would lay the groundwork for my dissertation.

At La Cañada High School, I found biology boring. I liked physics and German. My counselor advised me that German was the language of science (not true since Henry Baldwin's time), but I was more interested in football and cheerleaders. At the end of my junior year, I was selected as a Volkswagen exchange student to Germany. I stayed near the East German border, and drove to Berlin with my host family. Having the border guards train their automatic weapons on me helped me appreciate my sheltered life in America. The trip gave me a taste for travel and adventure I have yet to sate.

As my interest in marine biology grew, I started maintaining tropical marine aquaria at home, learned to snorkel, and took summer courses in marine biology at nearby Cal Tech. My grandparents sold the apartments on Balboa Blvd. and built a house at Three Arch Bay in Laguna Beach, where we spent many vacations. The clear waters of the rocky cove were ideal for diving, spear fishing, and exploring. I learned the fishes and invertebrates in what was arguably my real education. One spring break, shortly after I had seen *Jaws*, I was teaching my little sister to snorkel. I looked up to see my parents, shouting and pointing. In the clear water ahead, we watched a gigantic, dark shape approach, breaking the surface a mere 5 meters away. As it exhaled, I recognized it as a gray whale calf. I was so relieved not to have been eaten that I didn't get a chance to enjoy the spectacle as it dove underneath us. At 15, I took a SCUBA course with my father and bought my first single-lens reflex camera, eventually building an underwater housing.

The allure of underwater photography was outpacing my interest in science. In 1966, my favorite photographer, Ansel Adams, took a photograph outside where I now live in Santa Barbara, called *Birds on a Beach*. Intentionally cropped from the left of the photo is an offshore oil platform. I admired the Edenic style of Adams and in my photographs I also cropped out the blemishes in a way that idealized nature. After debating whether to study photography or marine biology, I concluded that one could be born with a talent for art, but to be a biologist required

schooling. Giving up photography school, I set up an interview with a professor at Cal Tech, but it was clear to him that I was not a good fit (they did little marine ecology). It would be the first of several rejections I would eventually be thankful for. UC Santa Barbara (UCSB) was the only university I could find that offered an emphasis in marine biology at the undergraduate level. After visiting the beautiful seaside campus, my mind was set and I enrolled as a freshman in 1981. My grades and athletic skills were sub-scholarship, but my parents generously contributed my rent and tuition.

The first quarter of my freshman year beer and recreational drugs were readily available, I got a punk haircut, stopped wearing shoes, played Frisbee every day, surfed, spun oldies records at the college radio station, photographed for the college newspaper, and did fashion modeling. In contrast, lower division biology was disappointing, given its lack of attention to natural history. With a full load of math and science, I did not excel. I learned to manage my time more effectively and pick and choose among my distractions (yes to beer, no to tequila). Upper Division courses allowed the level of specialization in marine ecology I was after. My GPA improved every quarter thereafter!

Money was tight, so I lived cheaply, sharing a small, one-bedroom apartment with a couple of roommates, hitting thrift stores for clothes, swap meets for surfboards, and garage sales for furniture. During breaks, I worked construction for my grandfather. One summer, I landed a job downtown as a parking lot attendant for the city of Santa Barbara. A couple of weeks into the job, I found out they were looking for SCUBA divers to help repair the local pier, Stearns Warf. The job paid twice the rate of a parking lot attendant, and I spent the day doing construction, but this time underwater. A local entrepreneur, Bob Meek, hired me to help him scrape mussels off the legs of offshore oil platforms and sell them to local restaurants. We worked in heavy seas and strong currents with little concern for safety. (Bob later died in a diving accident.) On my first day, I burst all the capillaries in my arm after it was sucked into the airlift we used to vacuum the mussels. Our air compressor sometimes pumped exhaust into our air supply and would quit when we were taking our decompression stops, requiring me to ascend and restart it. The job kept good food on the table. My roommate (and cousin) Tom worked at a French bakery and contributed fresh bread. The only downside of our gourmet lifestyle was its monotony. We could impress our dates with the first home-cooked meal, but the second, third, and fourth were just as likely to be steamed mussels and a baguette.

As graduation neared, I went to my boss and suggested that I was due a promotion. He balked, suggesting that I would first need a Master's degree. I was able to set up a 2-year program of coursework and exams in Ichthyology and Invertebrate Zoology at UCSB. Ironically, my job became less stable but I was eligible for teaching assistantships, and that paid enough to cover rent. I learned to enjoy teaching and turned my attention to becoming a high school biology teacher. My Invertebrate Zoology professor was Armand Kuris.

During a class field trip, Armand and I shared our passion for the natural history of the rocky intertidal zone. The next week, Armand asked me if I was interested in doing a Ph.D. in his lab. I had not previously considered a career in research nor did I have an idea about what a Ph.D. was about. I thanked him for the offer, but told him I already had a tentative contract to teach

biology. However, a few days later, during student teaching at the local high school, a bored student passed me a flirtatious note and I began to wonder if I was cut out to be a high school teacher. I realized I had built up an envious surfing lifestyle in Santa Barbara and had a hard time imagining myself teaching the Krebs cycle to 16-year-olds. I said yes to Armand's offer, primarily as a way to avoid growing up. Since I was already in the master's program, my acceptance was simply a matter of signing a form to switch tracks.

At that time, Armand was working on schistosomiasis, but he respected that I was interested solely in marine ecology. My first proposed thesis topic applied the intermediate disturbance hypothesis to the community of organisms that lived in mussel beds that I used to scrape. Several months into planning, I discovered that a dissertation had already been done. My first written qualifying exam was on rocky-intertidal ecology given by Armand, consisting of 3 questions, 1 of which could be skipped. When I reached the question: "Describe the role of parasites in the rocky intertidal," I blanked. Parasites had never been discussed in the papers I had read to prepare for my exam. I skipped it.

I then turned my attention to prawns. Armand had travel funds to investigate the social structure of freshwater prawns (*Macrobrachium rosenbergii*) in the Northern Territory of Australia and offered it as a potential dissertation system. An early test of our student-mentor relationship occurred while setting a trap line for prawns in the East Alligator River. At the parking lot, a sign read *KEEP CHILDREN AND DOGS FROM WATER'S EDGE*. I headed upstream and Armand headed downstream. As the last trap hit the water, I heard a second, much larger splash about 30 meters upstream. Imagining a saltwater crocodile headed my way, I turned and rushed for the bank as fast as I could. When we returned the next day for the prawns, one of my traps was missing and I told Armand that I must have let go of the line when I heard the mysterious splash. We had borrowed the traps, and Armand suggested that I try to recover it. I waded barefoot to where I thought the trap had landed, eventually touching it with my toes. Later, we found one of Armand's traps flattened with 2 holes the size of silver dollars. Clearly, a croc had been busy after all. The full-proposal was not funded, a disappointment that may have saved my life.

That winter, Professor John Endler, who had the lab next to ours, accepted a graduate student from Brazil who had just completed a Master's thesis on colonial spiders the size of golf balls. Cristina Sandoval looked nothing like the stereotypical Brazilian beauty. Her straight blonde hair and long legs had always been out of place at home, but fit my Californian tastes well. She needed help with her English and I felt well qualified to assist. We were dating before the ink dried on her passport stamp and I had yet another distraction to keep me from settling on a thesis topic.

I never earned a scholarship or more than a trifle in research support, needing to teach every quarter, including summer. That winter, I was in need of a teaching assistantship and Armand needed someone to run the lab sections for his Parasitology course. I had no interest in Parasitology and had not taken the course. There were no other teaching assistants and 3 lab sections, a brutal assignment. The collector, Shane Anderson, would bring in fish, sharks, sea urchins, octopus, and crabs and we would cut them up to look for parasites. I knew the natural history of the hosts but,

even after Bachelor's and Master's degrees in marine biology, had never learned about the parasites inside. Like my photographer hero Ansel Adams, ecologists had cropped out the blemishes of parasites when they told their story of nature. Teaching parasitology lab convinced me that parasitism was the norm and likely to be important, even beautiful. Ever since then, my efforts have revolved around bringing parasites into the bigger picture.

I discovered that a common crab had a diverse and abundant community of parasites and wondered whether they were important. For a year, I studied parasites of the spiny sand crab *Blepharipoda occidentalis*, a hideously armored beast of the surf zone with many interesting parasites, but eventually concluded that the system was intractable for a thesis. I then proposed to investigate whether infection with trematode metacercariae predisposed killifish to predation but decided the project was too risky. Ironically, I abandoned marine biology after 3 years into the Ph.D. program. My final dissertation proposal was to consider how behavior modification of cockroaches by acanthocephalan cystacanths might indirectly benefit rats by making cockroaches easier to catch. I modeled the interaction and planned experiments. I invited Al Bush, John Holmes, Andy Dobson, and Janice Moore to UCSB for seminars so I could get the perspectives of my parasitologist heroes. I set up a terrarium with cockroaches and started mastering the life cycle. I chose my committee, worked out a proposal with Armand, scheduled my oral exam, and sent out the proposal to my committee.

Two weeks before my orals, I realized the results I had predicted would be measurable only at the level of the rat population. A quick calculation of the animal care costs for doing the required experiments indicated that the project would personally bankrupt me. Without grant funding, I went to Armand to let him know I was dropping my fifth dissertation proposal. He reminded me that at UCSB the oral exam focuses exclusively on the proposal and without a proposal, there could be no orals. I asked him to wait a couple days before canceling the exam. The next day, I told Armand I had another idea and could get him a proposal by the end of the week. While teaching the parasitology lab, I had been fascinated with the community of trematodes infecting the mudsnail, *Cerithidea californica*. At Newport Back Bay, Walter Martin had worked out the life cycles and identification of more than a dozen species of trematodes from *C. californica* (Martin, 1972). Furthermore, Armand and Wayne Sousa had begun to look into the structure of this trematode community (Kuris, 1990; Sousa, 1990). I had read Dennis Minchella's work on how parasitic castration affected snail life-history strategies (Minchella, 1985), but little attention had been paid to how parasitic castration affected host population dynamics in the field. It seemed like an important question, and *C. californica* was the most tractable host system I could think of. The snails were easy to collect, keep alive, and dissect, and occurred in several nearby estuaries. Moreover, Armand liked the system and was prepared to overlook the last-minute nature of the proposal. I passed my orals.

There is a good reason Jacques Cousteau never did a documentary about estuaries. Compared to coral reefs or kelp forests, estuaries are stinky, muddy places with drab fishes living in turbid water. Throughout history, humans routinely filled them and converted them to dumps or harbors. As a result, in California, less than 10% of the original estuarine habitat

remains. However, I found estuaries fascinating. The bird communities are diverse and active. Invertebrates are common and easy to see. *Cerithidea californica* is a non-descript snail, generally coated with a fine layer of mud but often living in such densities that it is hard to avoid stepping on them. Dissections require little more technical expertise than swinging a hammer, something my construction background qualified me for. In a year and a half, I was done with the Ph.D. There were 3 main findings: (1) Snail density is lower where parasitic castration by larval trematodes is high; (2) snails living in areas with a high risk of being castrated tend to mature at smaller sizes; and (3) most estuaries are close to good surf breaks.

I was neither an accomplished writer nor a gifted mathematician but, for my first paper, I opted to write up the modeling I had done (modeling to understand ecology rather than to meet girls) on behavior modification I had developed for my failed dissertation proposal. Both reviews at the *American Naturalist* were positive (Lafferty, 1992). One was a brief paragraph signed by John Holmes, essentially saying publish "as is." However, my next several attempts at publishing my dissertation received mixed responses with extensive negative reviews signed by a particular reviewer. Teaching was looking better with each rejection. All throughout, Armand encouraged me to revise and resubmit. I learned to develop a thick skin and to take criticism as means of reevaluating and strengthening my work.

Although we had been admonished as graduate students that conservation biology was not real science, it was increasingly clear that ecology was needed to solve a growing list of environmental problems. I was particularly interested in fisheries and my dissertation system qualified me to study estuarine conservation. With research jobs scarce in the early 1990s, I paid the bills doing environmental consulting. I hustled for soft money. I was lucky to have a short part-time postdoctoral position to investigate a mysterious epidemic that was decimating local abalone populations (Lafferty and Kuris, 1993). I taught Parasitology and Invertebrate Zoology when Armand was on sabbatical.

An undergraduate, Kimo Morris, wanted to do an independent research project. I went to my file drawer of discarded dissertation proposals and pulled out number four, "Behavior modification of *Fundulus parvipinnis* by *Euhaplorchis californiensis*." Kimo and I went seining for infected killifish. We established an aquarium in the lab and I asked Kimo to watch the fish for a few hours and try to classify behaviors that caught his attention, the idea being that metacercariae on the brain might alter fish behavior to increase susceptibility to final host birds. Kimo returned with a list of conspicuous behaviors. We went seining again, but this time at a location that lacked the first intermediate host for the parasite and mixed them with the infected fish. Kimo tracked an individual fish for 30 min, recording its behavior. If he lost it in the school, he started over. Afterward, he captured the fish and dissected it. We plotted the data and saw that the infected fish had 4 times the rate of conspicuous behaviors as the uninfected fish. Furthermore, conspicuous behaviors increased with parasite intensity. This was strong evidence of manipulation, but such patterns had been demonstrated before. We then asked if birds would preferentially prey on infected fish. We set up schools of fish in pens in the Campus Lagoon, covering one of the pens with netting. We watched herons and egrets feeding in the open pen. After several days, we brought the pens to shore and dissected the fish in the closed and open pens. By comparing parasitism in the

2 pens, we estimated that infected fish were 10–30 times more susceptible to predation by birds (Lafferty and Morris, 1996). We now had a strong argument that parasites affected something that many ecologists cared about—bird food. Kimo ultimately earned a Ph.D. at UCLA.

There were no job advertisements for ecological parasitologists and I did not garner interviews at even the most obscure teaching colleges. At the Ecology meetings in Honolulu, I saw a post for a postdoctoral opportunity at Cambridge to work with parasites of Soay sheep in western Scotland. Before the interview with Bryan Grenfell, I was out surfing, and lost track of time. Rushing back, I saw a fellow graduate student and swapped my board for his shirt so I could meet with Bryan clothed. Bryan must not have noticed that my shorts were soaked (he has famously bad vision) and invited me out for a seminar and visit. But Cambridge was too cold for my Brazilian girlfriend.

Cristina and I were married in Brazil in 1992. Shortly after, Cristina finished her Ph.D. and was offered faculty positions, including at the University of Florida. Since none was perfect, we stayed in Santa Barbara, began to build a life there, and kept looking for other jobs. At Ecology meetings in the 1990s, my talks would be slotted in miscellaneous sections with other lightly attended, misfit topics. It was not an encouraging indication of the appeal of ecological parasitology.

In 1994, I attended my first American Society of Parasitologists meeting in Fort Collins. Al Bush helped me gain admittance to the smoky hotel rooms where cans of Budweiser were kept chilled on ice in the bathroom sinks. My presentation was on a paper Armand and I were writing about the structure of larval trematode communities in *C. californica* (Lafferty et al., 1994). Our conclusion of strong competitive interactions in these communities was at odds with both Sousa and Esch's work, so I was a little concerned about how it would be received. Al Bush approached me to say that Jerry Esch had a special project in mind. The 1982 paper on population terms in parasitology by Margolis, Esch, Holmes, Kuris, and Schad had proved a surprising Citation Classic for the *Journal of Parasitology* and Jerry felt it needed updating. Jerry's idea was to get a new generation of ecological types to develop a sequel that expanded the concepts to parasite communities. Al Bush, Jeff Lotz, Al Shostak, and I met at a local bar where Al Bush carved up the assignments. Due to my junior status, I was given the easiest term (Prevalence) and tasked with the graphics. The paper (Bush et al., 1997) has become the most highly cited article in the history of the *Journal of Parasitology* (Trivia question: What is consistently the least cited type of article published by the *Journal of Parasitology*? Answer: *The acceptance of the annual Henry Baldwin Ward Medal*). At the end of the meeting, Jerry offered me a ride to the airport. He turned on the air conditioning and asked if I minded if he smoked. I lied and we were able to find considerable common ground on trematode communities during the drive.

I landed a research position at UCLA to design and conduct coastal monitoring programs. Not having the stomach to leave Santa Barbara, I commuted the 100 miles several times a week. In 1995, my first daughter, Olivia, was born, and my wife and I volunteered to be residential caretakers of the University of California Natural Reserve at Coal Oil Point near UCSB. We lived rent free in an ancient singlewide. The door would not lock and the trailer was infested with rats (too late to rescue my failed dissertation project), but the 73 ha coastal property included my 2

favorite surf breaks. Our second daughter, Bela, was born shortly after we moved in. Eventually, we upgraded to a modern doublewide and my wife obtained a directorship position to develop education, conservation, restoration, and research programs at the reserve. We live there still.

In 1998, I finally landed a dream job at the Western Ecological Research Center of the U.S. Geological Survey. Despite its name, the USGS employs a large number of research biologists to address the science needs of the U.S. Department of Interior (this includes the Fish and Wildlife Service and the National Park Service). The position was located in Ventura, an hour south of my house, in the offices of the Channel Islands National Park. Historically, the marine ecologist in that position had provided science support for the marine resources in the park and I began a research program to help recover endangered white abalone. A few months into the job, the Park Superintendent told me that he was short on space and needed me to share an office with several other technicians. I told him that I still had some space at UCSB and would be happy to work from there if it helped him out. It solved his space problems, and I returned to the university. Armand allocated me some of his space and the university gave me adjunct faculty status so I could mentor graduate students. Back at UCSB, hanging out in Armand's lab, I felt the pull of parasitology again. My supervisors agreed that I could work on parasites so long as I first fulfilled my expected contributions to the Department of Interior.

Not everyone dislikes parasites. Famously, in *Casa Blanca* (1942), the pragmatic Rick (Humphrey Bogart) says to Ugarte (Peter Lorre), "I don't mind a parasite, I object to a cut rate one." I admire parasites, particularly first-rate ones. My favorite is probably *Toxoplasma gondii*. This protozoan infects nearly every warm-blooded vertebrate, placing it on all oceans and continents, even in the skies. It preferentially encysts in the brain and appears to manipulate behavior. It infects from a third to one half of the world's human population. After publishing a paper on the hypothesis that *T. gondii* alters human culture (Lafferty, 2006), I went to the local clinic to be screened for antibodies. I was somewhat disappointed (and felt a little lonely) to be negative for the antibodies. I like other parasites too, trematodes in particular. Nevertheless, I prefer the jack-of-all-trades label with its attendant master of none drawback. I have worked in estuaries, coral reefs, streams, kelp forests, and tropical forests. I have cut and counted as well as built mathematical models and scoured the literature for meta-analyses. I am interested in climate change, fisheries, pollution, biodiversity loss, habitat restoration, evolution, endangered species management, food webs, and behavior. I have learned that parasites fit into all these places, approaches, and topics.

It has been a better career than I could have imagined. Over the years, the USGS became increasingly supportive of my parasitology work and parasites have returned as my research focus. In turn, UCSB came up with additional space and resources for me to develop an independent research program. I have a permanent, 12-mo, federally funded research appointment with only 1 university service responsibility (faculty advisor to the UCSB surf team), making it easy to find time to write papers. My position has opportunities for adventures and I have been able to travel to 250 cities in 26 countries, often with my surfboard. Moreover, there is the sort of fame only a parasitologist can achieve. After Carl Zimmer interviewed me for his popular book

on parasites, I have regularly received mail, phone calls, and various samples in vials from people seeking help with their imagined parasite infections or tattoo plans. One letter from a convict sought my advice on how he might use toxoplasmosis in an insanity defense against a recent burglary spree. I told him he could get a blood test, but it was more likely the meth than that toxoplasmosis that was to blame.

The path of my career was not traveled alone. My parents were always supportive of what I wanted to do, providing me opportunities to learn about biology and obtain the education that I needed. My friends put up with my eccentricities and unstable career choices as they pursued respectable professions. My wife gives the understanding only another scientist can offer while my daughters have been patient (and darling) students, helpers, and surf partners.

At the top of my 74-long coauthor list is Armand Kuris. We spend so much time on the phone that Armand's wife, Bari, jokes we must be having an affair while my wife is jealous of the "quality time" I spend with Armand. Students sometimes mistake Armand for my graduate student (until they meet him). Armand runs a hands-off, egalitarian, and democratic operation. He values and encourages original thought over directed mentoring, which means some students flounder while others flourish. With 6 dissertation topics, I nearly floundered, but Armand's encouragement gave me the confidence to seek out new questions and research directions. Armand and I differ considerably on style (though after many years he finally stopped tucking T-shirts into his shorts), but we agree on our key values: our congruent view of parasite evolution, and the importance of adventure, natural history, creativity, excellence, originality, ambition, loyalty, and family. I am truly proud to see him recognized as both this year's Eminent Parasitologist and recipient of the 2010 Clark P. Read Mentor Award.

Tied for second on my coauthor list are Mark Torchin and Ryan Hechinger, former Kuris students and polar opposites in many regards. Mark is shorter than me, a sly jokester, and balanced family man. Ryan, this year's recipient of the young investigators Ashton Cuckler Prize, is frighteningly large, proudly eccentric, and keeps long and odd hours dedicated fiercely to parasitology. I have spent many hours surfing with each and I'd want either with me in a dark alley. Andy Dobson from Princeton comes in fourth. Andy is a consummate British gentleman and poly-talented scientist, the sort of guy you want to have as the best man at your wedding. Armand's student Todd Huspeni (who still tucks his shirt in his shorts), and my students Mike Behrens and Jenny Shaw, tie for fifth and have been wonderful partners in

science. Many of my recent collaborators are scientists I have met at the National Center for Ecological Analysis and Synthesis, an ecological think tank located in downtown Santa Barbara. I could go on and on because any success I have achieved has been founded on solid mentorship, productive collaborations, and motivated students.

To conclude, parasitology is not a field I was drawn to or intended to pursue—it was an accident. My career path has been unstructured and without program or plan. Circumstance, opportunity, and timing dictated how things played out. My main contribution was preparation and an open mind. Though I did not shape my career, it has shaped me. I feel fortunate to study parasites at a time when their ecological importance is increasingly recognized. I have not collected many awards in my career but, if I could only have one, it would be the Henry Baldwin Ward Medal.

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