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ACCEPTANCE OF THE HENRY BALDWIN WARD MEDAL FOR 2018: A FASCINATION OF THE ABOMINATION

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Good afternoon. I want to sincerely thank everyone for coming today, particularly in light of the many potential distractions afforded by this venue. It really is an honor and a pleasure to be here. I want to begin by thanking Dr. David Marcogliese, who was the 2001 recipient of the Ward Medal, and Dr. Cam Goater, both of whom went to great lengths to nominate me for this distinction. Beyond the nomination itself, I am grateful to them for their insights, guidance, and enthusiasm over the years, tracing all the way back to my early days as a graduate student. And, of course, thank you to Dr. Janet Koprivnikar for that enlightened and only slightly embarrassing introduction. More importantly, I thank her for being a dedicated collaborator and co-conspirator throughout much of my scientific career. Our interactions have taught me more about parasites and parasitology than any class or textbook, including their remarkable suitability for being featured in cartoons. Even within a field known for its nuanced sense of humor, Janet is in a league of her own—which I mean in the best way possible.

Traditionally this presentation is focused on telling the scientific and personal journey of the award recipient. Sitting down to do this was much harder than I expected—you come to realize how much we focus on the presentation of our science, rather than our own story and experiences. Being an academic, I naturally looked to past recipients for inspiration. This, unfortunately, made developing my own comments exponentially more difficult; reading over the past speeches was a remarkably humbling endeavor. Truth be told, I have often felt like a bit of an impostor at these meetings. I am not a parasitologist, or at least not in the classical sense. I have never taken a parasitology class, nor were any of my official graduate or undergraduate advisors trained in the field. But one thing that has long-amazed me about the field of parasitology generally, and the American Society of Parasitologists (ASP) in particular, is its welcoming culture. The number of “card-carrying” parasitologists—including many folks in this room—who have gone out of their way to help me over the years is astounding. And while I didn’t realize it early on, the legacy of Henry Baldwin Ward has gently supported me through much of my career, as I will revisit later.

A FASCINATION OF THE ABOMINATION

When asked to give a title for my talk today—which admittedly was several months ago—I elected to use “A Fascination of the Abomination,” which traces back to Joseph Conrad’s novella *Heart of Darkness* (Conrad, 1899). It alludes to people’s near-pathological need to look upon or experience things that are arguably horrific. Whether it’s rubbernecking at an accident scene, watching a horror movie, or riding a roller coaster, humans have a strange inclination to flirt with terror. This fascination often involves a complex set of emotions—relief that the event in question hasn’t happened to us combined with the fear that, one



day, it could. Yet Conrad’s book was also about a quest into the natural world, and when it comes to science, a key additional motivation for this fascination is to understand how, precisely, such things happen. Nineteenth-century scientists were obsessed with studying morphological variation and its role in natural selection (e.g., Bateson, 1894), including the evolutionary potential for hopeful monsters or non-gradual jumps in development (Van Valen, 1974).

Ultimately, my intrigue for parasites comes from this fascination of the abomination. What I mean here is not that parasites are horrific or frightening per se (even if many find them so), but more about the remarkable and awe-inspiring things that even seemingly invisible organisms can do to individual hosts, to communities, or even ecosystems. Who needs science fiction when we have parasitology? (Although I confess I’m a sucker for creature flicks.)

As part of this talk, I had to ask the question—how did I first become interested in parasites? I was supposed to become a marine biologist. My family is from southern California, and we spent most summers camping at Carpinteria State Beach—and, yes, that’s the same Carpinteria made scientifically famous by the research of Drs. Armand Kuris and Kevin Lafferty. Long before I’d ever thought about parasites, I would head out to the tidepools at dawn—often armed only with a flashlight and a bucket—and spend as much time as the tide would allow. This instilled in me a deep love of biology for all of its diversity and especially its mysteries. You really never know what the retreat of the tide might expose on any given morning.

Because we couldn’t camp all the time, I used money earned from my paper route to establish temperate reef tanks in my parent’s living room, often combining various aquaria and old mini-fridges from garage sales. I learned a lot about species coexistence in those days, and specifically which species didn’t play well with one another. Over the years I kept octopi, spider crabs, stingrays, leopard sharks, sea anemones, urchins, and countless others. I further discovered that some animals are much

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more difficult to keep contained within an aquarium. This was Mom's least favorite part—coming down to make coffee in the morning only to find an octopus oozing across the kitchen floor still gives her nightmares.

As soon as I was 12, I became SCUBA-certified so I could observe these animals in their natural environments. It wasn't long before I was enrolling in marine programs, and I spent various summers developing artificial temperate reef systems off the coast of Newport, tracking sea urchin movement at the Hopkins Marine Station, studying sculpin tidepool fidelity at the Oregon Institute of Marine Biology, and working as a research diver for the Australian Institute of Marine Sciences in Queensland, to name a few. One of my earliest and only sole-authored papers was on biased sex ratios in fiddler crabs, which included one of the most elaborate yet unsuccessful experiments in history (Johnson, 2003). So perhaps I wasn't cut out for marine biology after all.

A FLUKE OF NATURE AND THE THREE PAULS

A watershed moment came while I was an undergraduate at Stanford University looking for an honors thesis project. My plan had been to return to Hopkins Marine Station when a curious thing happened. In August of 1995, a group of Minnesota middle-schoolers on a class field trip stumbled across a pond in which half of the emerging leopard frogs were deformed. Many of them exhibited severe limb malformations, such as extra or twisted limbs. Given the nature of the story—with school-aged children discovering apparent mutants in a farm pond—this turned into a category 5 media storm, aided by the dawn of the internet. Soon after, reports began to flood in from across the country. While a low frequency of deformities can be expected in any population, this baseline rate is typically low, maybe 2%, and it was the combination of the severity of the malformations along with their high frequency that alarmed citizens and scientists alike.

Numerous hypotheses and even more hyperbole were advanced: were the malformations the result of ultraviolet radiation, pesticides, hormone mimics, inbreeding, industrial feed operation waste, or something more sinister? The driving concern was that whatever was causing deformities in frogs could also threaten humans. Around the same time as events were unfolding in Minnesota, a local landowner near Stanford reported a high frequency of deformed frogs on his property—30 to 50% of the emerging animals, including abnormalities in multiple amphibian species. Talk about fascination of the abomination! This was a dream project for an undergraduate thesis—there had to be an answer, and really, any answer was interesting. The question was whether I could find it. The ponds happened to be on an ostrich ranch, which somehow made the story that much more irresistible. Putting my marine research plans aside, I began examining thousands of amphibians, not just from local ponds but sites all over the county, meticulously describing the types and patterns of malformations—how they varied over time, among frog species, and what features were shared among areas where they occurred.

Mostly this was a story of null data and false starts—the leads or approaches that don't work out but hopefully teach us something in the process. Like most people, I initially assumed that there was a contaminant in the water. With the help of encouragement and funding from my undergraduate advisor, Dr. Paul Ehrlich, I tested the water for a wide range of pesticides and

heavy metals, but ultimately found nothing unusual. Raising eggs of amphibians in the laboratory led only to normal tadpoles, suggesting the cause was environmental rather than genetic. This observation was consistent with the detection of malformations in multiple species simultaneously. Frustrated I wasn't making more progress, I returned to the microscope to continue cataloging the specific aberrations of each frog, no two of which were exactly alike in their deviations, which led to an intriguing clue: just beneath the skin of affected animals were tiny, cyst-like structures that were especially visible through the semi-transparent tissue near the hind limbs of tadpoles. These cysts were more common at ponds with high levels of deformities.

Yet determining the identity of these elliptical structures would prove elusive. Graduation was rapidly approaching, so I reached out to the Stanford Medical School for help and advice. By a stroke of luck, I was put into contact with Dr. Paul Basch and even managed to convince him to take a look. As some of you know, Paul was a talented parasitologist, a long-term member of ASP, and a distinguished schistosome researcher. He was also remarkably generous with his time. Not many Stanford Medical School professors would have come across campus to visit the makeshift lab space of a pesky undergraduate. It was Paul who put us on the path that eventually identified the mystery cysts as metacercariae of the trematode *Ribeiroia ondatrae*. Remarkably, Paul had published on the life cycle of another species of *Ribeiroia* from Puerto Rico in 1969 (Basch and Sturrock, 1969), which remains one of only two papers on the life cycle of this group. That species had earlier been described by Dr. Ernest Faust (Faust and Hoffman, 1934), who was one of Henry Ward's early graduate students.

As further evidence of Ward's legacy, one of his other students, Dr. Paul Beaver, described the life cycle of *R. ondatrae* in a 1939 monograph that became very influential in our research (Beaver, 1939). Paul Beaver, as it turned out, also chaired the committee that first established the Ward Medal in honor of his former advisor, so I need to thank him on multiple fronts. This breakthrough led to a crash course on parasites generally and trematodes in particular, and after a lot of missteps, including experiments with the wrong parasite, the wrong dosages, and the wrong experimental design, we were finally able to test how *Ribeiroia* cercariae affected amphibian limb development under controlled conditions. It was a startlingly simple experiment, but one that would make me an experimentalist for life.

Incredibly, even small numbers of cercariae caused upwards of 50% malformations among exposed tadpoles. The severity of the abnormalities encompassed all of the forms we saw in nature—from no hind legs whatsoever to as many as 6 extra limbs (or 10 legs in total). Subsequent field work helped show that the abundance of *Ribeiroia* per frog was a strong, positive predictor of the malformation frequency at natural wetlands. At sites without *Ribeiroia*, abnormalities were rare and typically within the expected baseline range; at sites with the infection, the frequency and severity of deformities increased in direct relation to average infection load, sometimes affecting nearly every emerging frog (Johnson et al., 2002).

The underlying science behind this work was not especially remarkable or ground-breaking. Because of the controversial nature of the topic, however, the study ended up being published in *Science* (Johnson et al., 1999), where it garnered widespread media attention (e.g., Kaiser, 1999). Three of the four authors were recent undergraduates: myself and two friends (Kevin Lunde

and Euan Ritchie) that I convinced to spend their waking hours devoted to the project if I provided food and housing. I'm embarrassed to admit it wasn't very good food or housing; we lived in an unfurnished studio apartment with shag carpeting and a cardboard-thin front door that sprang open every time a train went by, which was approximately every hour.

LOOKING BACK ON LESSONS LEARNED: WHY PARASITOLOGICAL RESEARCH IS CONTAGIOUS

From there I went on to pursue a Ph.D. at the University of Wisconsin working with Steve Carpenter, an ecosystem ecologist renowned for his work on aquatic eutrophication as well as trophic cascades. Naively, I had always assumed that, after "finishing" the deformed frog work, I would be done with parasites, perhaps heading back to marine biology. But I had underestimated the magnetic appeal of parasite research and its capacity to captivate the imagination. Almost without realizing it, my research program began to coalesce around the core goal of building parasites and pathogens into community ecology research, a topic on which there was surprisingly little integration at the time. My Ph.D. ultimately focused on how aquatic eutrophication influenced parasite infection and the role of fungal epizootics in lake food webs. I even managed to convince Tim Yoshino—former ASP president, member of the faculty at the UW Veterinary School, and 1999 recipient of the Ward Medal—to join my dissertation committee and collaborate on a project investigating the effects of host diversity on transmission of schistosomes, which would help shape a major subsequent chapter of my research program.

As I was finishing my Ph.D. in 2006, I was offered a faculty position at the University of Colorado in Boulder, which was too good an opportunity to pass up. I was fortunate with funding, including a fellowship from the David and Lucile Packard Foundation and a CAREER grant from the National Science Foundation, which provided the intellectual and financial freedom early on to push ahead on a range of topics at the intersection between community ecology and disease ecology. I set out to better understand the "hidden" influence of parasites in shaping ecological communities and ecosystem processes, and, reciprocally, examining how host-parasite interactions were affected by the complexity of "real-world" systems with multiple hosts, coinfecting parasites, and predators. This included field and experimental studies on topics such as predator-parasite interactions, biodiversity effects on transmission, interactions among coinfecting parasites, and the response of parasites to climatic extremes. While much of this work has focused on freshwater habitats, more recently I've even managed to build in more marine parasites—perhaps coming full circle after all. Studies of the trematode *Scaphanocephalus expansus*, which causes black-spot syndrome in tropical fishes, and the cymothoid isopod *Olencira praegustator*, which invades the mouths and gills of Atlantic menhaden, have both helped to satisfy my ongoing "fascination of the abomination."

But rather than go deeper into my research history or plans for the future, I elected instead to consider what lessons and insights have most influenced my career path, broadly keeping in the tradition of past Ward recipient presentations. Three are worth emphasizing, all of which were strongly molded by my chaotic early experiences with parasites.

THE POWER OF STUDENT SCIENTISTS: WHY THE BEST SCIENTISTS ARE STUDENTS

One of the most enduring lessons for me has been the power of student scientists. Junior scientists are among the most flexible in their capacity to pursue new leads and dynamically change direction when needed. They are the true definition of cross-disciplinary scientists, untethered by inertia or job title, and I have learned to listen carefully to the thoughtful insights and inspired connections made by my students, even when they initially seem far-fetched. While a student myself, there was even something surprisingly liberating about having little money or resources to do science. After finishing the experimental work at Stanford, Kevin Lunde and I borrowed my parent's 1983 Ford Econoline van and embarked on what would become a 10,000 mile trip crisscrossing the western and midwestern United States. We sampled hundreds of ponds and thousands of frogs to test the link between infection and malformations, motivated in part by the disparagement of established scientists telling us we couldn't do it or it wouldn't work (e.g., Johnson et al., 2002, 2003).

Building on these experiences, I've endeavored to establish my own lab at the University of Colorado around this core value of creating a collaborative environment with students of diverse experiences and research interests, from undergraduates through postdoctoral researchers. They regularly and repeatedly do the impossible, and I continue to learn as much from them (and likely much more so) as they do from me. I thus want to thank the members of my lab, both past and present, who have had such a profound impact on how I view science and the world. Most especially, I thank Sara Paull, Sarah Orlofske, Katie Richgels, Bryan LaFonte, Max Joseph, Dan Preston, Jason Hoverman, Dana Calhoun, Joe Mihaljevic, Sarah Haas, Jason Lambden, Ian Buller, Keegan McCaffrey, Travis McDevitt-Galles, Wynne Moss, and Kelly Loria. They have been the intellectual engine of the lab as well as its cultural heart. I've elected not to include any embarrassing photos or stories here with the knowledge that they are also very creative in devising payback.

And, of course, the student scientists who have taught me the most about the nature of inquiry are my own children, Katelyn and Kyle. Viewing the natural world through their eyes reminds me why biology is so amazing and in such need of conservation. Their pure enthusiasm and boundless passion continually also make field work much more exciting and unpredictable, albeit a bit more time-consuming than usual.

SCIENCE AS A CHARITABLE ENTERPRISE

Second is the idea of science as a charitable enterprise. One quickly and inevitably comes to realize how much of science depends on the help and collaboration of numerous individuals. No one has supported me more than my parents, Richard and Joke, who have unfailingly encouraged my scientific interests and pursuits—even when they have quite literally transformed entire sections of their house into makeshift laboratories. And that's not even mentioning the parades of octopi across the kitchen floor or the state of that old Ford van when it was finally returned, 10,000 miles later.

In the professional world, I am grateful for the extraordinary generosity of those scientists who have continually contributed to my own education over the years as well as those of my students.

The perspective of time makes abundantly clear how much these individuals have done on my behalf, and I think about their examples frequently as models for my own behavior. Two examples warrant mention: Dr. Andrew Blaustein, a professor at Oregon State University, has mentored and supported me for over a decade, even though I was never officially one of his students. Perhaps more than any faculty mentor I've ever encountered, Andy is fiercely devoted to his students both professionally and personally. I first met him 17 years ago when I was an undergraduate presenting at a special NSF workshop on amphibian deformities. I was lucky to have made the roster, and I remember both my naiveté and excitement at finally sharing my research with others. To my crushing disappointment, however, several scientists attending the meeting were less than thrilled to have “unproven upstarts” present evidence contrary to their own programs, and I was soon fending off a frenzy of critiques ranging from confounded experimental design to outright fabrication. (“They’re only undergraduates” was an attempted coup de grâce.) Andy stood up and—despite barely knowing me—defended the ecological relevance of the research and its integration of field as well as experimental approaches, effectively redirecting the entire discussion. That hour was pivotal to my decision to pursue science as a long-term career choice. Over the years that followed, Andy has always reminded me that while science in practice isn't perfect, its arc of knowledge bends eventually toward truth (to roughly paraphrase MLK).

The second individual is Dr. Daniel Sutherland, who was a parasitologist at the University of Wisconsin, La Crosse. It was Dan who really taught me to love parasites and think deeply about the nature of parasite communities within hosts. He had the nickname of “gut pile” because of his predilection—no doubt shared by several people at this meeting—for processing any and all kinds of roadkill for parasites. When he wasn't dissecting the unfortunate victims of highway collisions in his garage, we spent many hours tromping through leech-infested swamps together, which remain some of my favorite field moments. Dan also had the most incisive sense of humor I've encountered, which stayed sharp all the way through his untimely passing in 2006. Just before his death he suffered a massive stroke that damaged a major part of his brain. After the doctors told him about it, he nonchalantly responded, “That's okay, that's just the part of my brain where I store my in-depth knowledge of statistics.” I am grateful for the time we had together and wish it had been longer.

A LABOR OF LOVE: WHY SCIENCE SHOULD BE FUN

My final point is obvious but all too forgettable: science ought to be fun. None of us are paid enough to justify the hours we invest, so if you don't love what you do you're probably in the wrong career. For me, science has always been a team sport—something both more productive and vastly more enjoyable when done alongside those you like and respect. Choosing the right collaborators is perhaps one of our most important yet most challenging skills. While I have long had a tendency to be task-focused, it is my collaborators who have reminded me of the big picture, both scientifically and personally.

I have been lucky enough to do science with some of my best friends, and to be friends with individuals that rank among the best scientists. One of those is Dr. Kevin Lunde, who's been a friend, collaborator, and co-conspirator since we were 5 years old.

We have been inseparable friends ever since, including best men at each other's weddings. His ability to catch frogs is outmatched only by the depth of his loyalty to his friends. I would not be where I am today without his unshakeable personal as well as professional support.

And finally, I want to thank my wife and partner, Stefanie Johnson, who is a professor in psychology and business. But she certainly deserves an honorary degree in biology for all of her efforts (and patience) working alongside me. She more than anyone continues to offer the keenest scientific insights into my own work, despite (or perhaps because of) her contrasting background. Fittingly, we just published our first paper together—on how *Toxoplasma gondii* exposure is associated with patterns of business entrepreneurship in students and among nations (Johnson et al., 2018)—an appropriate way, I think, to celebrate our 12-year anniversary.

LOOKING FORWARD

This is an interesting time for parasitology. Arguably the study of parasites and pathogens has never been more important than it is today. There is growing demand as well as opportunities for scientists that can effectively integrate the independently evolving literatures of parasitology, community ecology, and epidemiology. Yet, at the same time, we confront worrisome issues surrounding a shortage of scientific funding, waning membership numbers, and a lack of suitable faculty positions. The priority, therefore, centers around training our students to embrace the interdisciplinary approaches and tools necessary to succeed in solving tomorrow's challenges. Doing this—not just accidentally, but deliberately—requires recognition that the template for success in the next generation will not be modeled solely upon the scientists of today. Shaping our students to transcend the limits of our own approaches and perspectives is a goal we must keep at the forefront for their sake as well as our own.

I want to conclude by thanking President Perkins and members of the Society, both present and past, for the remarkable honor of being included in the esteemed company of previous Ward Medal recipients. It is humbling to look upon the breadth and depth of parasitological research that precedes us; an hour with the literature truly is worth a month in the lab, or even an entire summer in the field. Appropriately enough, I wanted to end with a quote from Henry Ward's address at the first ASP meeting in Kansas City in 1925, which was entitled “Needs and Opportunities in Parasitology” (Ward, 1926). Many of the topics are still relevant and worth revisiting. Among my favorite quotations is the following: “Desk work has a clearly subordinate value in biology and neither in teaching nor in research shall we make adequate progress unless we follow the admonition of Agassiz and stick to our specimens until we know them” (p. 234).

This is a worthwhile reminder to us all to remain intimately connected to the natural world around us. Thank you all for your attention.

I would like to thank David Herasimtschuk, Freshwaters Illustrated, for generously allowing use of the photograph.

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