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ACCEPTANCE OF THE 2021 HENRY BALDWIN WARD MEDAL: PARASITE FORMS MOST BEAUTIFUL

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President Tkach, ASP members, colleagues, and friends, I am incredibly humbled to be counted among the recipients of the Henry Baldwin Ward Medal. It is truly an honor to be here today. I wish it could be in person, but I am thankful that we can use virtual technology to gather, despite the devastation and uncertainty caused by the current pandemic. In preparation for today, I was looking through the addresses of previous Ward Medal awardees. In so doing, I found a common theme: *Parasitology is often what happens when you are making other plans*. Thus, in the tradition of these addresses, I will share my plans, what actually happened, and a few of the lessons I learned along the way.

My path to biology began with art. In order to draw an organism and make it identifiable, you have to understand its form and how to represent that form in a way that is unique from other similar forms. As an artist you must use colors, shapes, and lines to create representations of each organism you illustrate. Gross changes may separate distantly related organisms, whereas slight details may be needed to distinguish closely related species. Only recently have I realized that it is a small, logical step to go from drawing distinct forms to wondering how those forms came to be. Evolutionary biology provides compelling answers to this question. In the final line of *On the Origin of Species*, Darwin said "from so simple a beginning endless forms most beautiful and wonderful have been, and are being, evolved" (Darwin, 1859). Parasites are no exception. They are diverse. They are beautiful. They provide exciting new opportunities to understand the evolution of biological forms. It took time, however, for me to discover parasites as the beautiful, evolving forms they are.

My parents nurtured an appreciation of nature. We went on many road trips, and we camped a lot. Our family would build lists of species seen on each trip, and, as incentives for paying attention, my sisters and I would earn 10 cents for each new bird species that we spotted. Sometimes we would earn a quarter if we spotted wildlife that was harder to find, like a moose or a beaver. My father taught us the Latin names of trees, although I later found that many of the names he taught us had long been synonymized. Even my favorite name, *Pseudotsuga taxifolia*, which rolls off the tongue, is no longer considered a valid name for Douglas fir. Occasionally, if I did not know the scientific name for something, I would just make up a new one. I now know this violates the International Code of Zoological Nomenclature, and I have learned to assign new scientific names properly.

Our family would often head out early on a Sunday morning to the local woods or red rocks to paint. Watercolors in hand, we would spread out through the landscape and paint for a few hours. During our mid-morning coffee break, we would line up all of the work, receive a critique, then head out again to continue or start afresh. I preferred to draw organisms: flowers, leaves, birds, and bugs. I especially liked getting up close to capture the details.

I was drawn to biology. In high school I signed up for as many science classes as I could. To this audience, this probably seems like the logical progression. However, this was not the case. Why? I grew up as a female in Utah. Even to this day, Utah routinely ranks last in the country for women's equity. Women trail behind men in wages, leadership roles, and education, especially in STEM (Jacobs, 2020; McCann, 2020), even though Utah has improved considerably in the last 40 years. There are many reasons for this inequity, but a large part of it derives from the patriarchal structure of the predominant religion in the area. I grew up in the county in Utah that is home to Brigham Young University, one of the main epicenters of The Church of Jesus Christ of Latter-Day Saints, or "Mormons". Most of the people in the community I lived in were Mormon, most of the kids in school were Mormon, and I was raised Mormon (although as coffee drinkers, and sometimes Irish-coffee drinkers, my nuclear family was certainly on the more liberal outskirts of the religion).

When I was about 15, the local Mormon bishop called me into his office. This was not a good sign. I was expecting a scolding for my mere monthly attendance at church or bad caffeine habits. Those topics did arise, but to my surprise, the bishop had my high-school class schedule. "I understand you are taking chemistry, biology, and calculus next year, but you are not signed up to take the LDS seminary course," he stated. (Now, for those of you who did not grow up in Utah, the LDS church typically owns a building adjacent to public high schools where students can attend an off-campus seminary class that just happens to be synchronized with the public-school schedule.) Looking down at me over his reading glasses, he continued: "You do not need these science and math classes. You need to take seminary so that you can become a good little wifey." I was stunned. "Wifey" should not be a word, and was certainly not something I ever wanted to become. I explained I needed science

Figure 1. Doing fieldwork on San Salvador Island, Bahamas.

and math more than I needed religion. I left his office, and I left the church.

Anger fueled ambition. I was going to show the patriarchy how wrong they were. Women belonged in science. I belonged in science. I was fortunate because I had parents and teachers who supported my scientific ambitions. I was fortunate because I did not have to flee communist regimes to pursue my interests, like Vasyl Tkach and Matt Bolek (both former Ward Medal recipients; Tkach, 2017; Bolek, 2019). It is important to recognize, however, that despite our "free" society, there are visible and invisible barriers that prevent equality and prevent or deter people from pursuing their interests. We all need to encourage and support others around us, and even small actions can make a huge difference. For me, this came as a note from my high-school biology teacher. One day, Mr. Reese wrote on the top of one of my assignments "You're good at this, keep going." This simple note reached me at a time when I really needed it. It was affirmation from someone in science. I felt that I belonged. (There is now a Chinese acanthocephalan named in his honor: *Pseudoacanthocephalus reesei* (Bush et al., 2009)).

I poured everything I had into studying biology in Mr. Reese's class. We covered the entire *Biology* textbook by Curtis and Barnes (5th Ed.) 3 times. We learned biology. We breathed biology. We dreamt biology. In the entire class, my favorite section was about peppered moths (*Biston betularia*) and the change in color-morph frequency that followed the industrial revolution in the U.K. I was taken by the classic image of light and dark forms attached to different colored tree trunks. It was a biological yin and yang, light and dark forms oscillating based on conflicting forces. The forms were beautiful, and the forms had function. Moths that did not match the background were more conspicuous and were more likely to be eaten by predators. The dark form was first reported in 1848. Forty-seven years later, 98% of the moths in soot-covered Manchester were the dark form (Kettlewell, 1958). The evolution of drastically different forms had happened within just a few decades. This was amazing! Biology had answers, and I wanted to help discover them.

With encouragement from Mr. Reese, I applied for summer research programs. Thanks to the Howard Hughes High School program I was placed in Dr. Ryk Ward's lab in the Department of Human Genetics at the University of Utah. I learned cutting-edge technology: Sanger sequencing. Another high-school student and I worked all summer to get DNA from human blood samples. I was ecstatic when I finally got a readable gel with more than about 50 base pairs. This was a part of a serious research effort, and I was contributing sequences to a paper that ultimately included 360 mtDNA base pairs from 82 individuals (Ward et al., 1996) from 3 indigenous tribes. The project was using genetic data to trace the history of lineages and build phylogenetic trees. Other members of the lab were using similar methods to study the evolution of Bornean tree frogs and North American carnivores. I wanted to be a part of this type of research. Mistakenly, however, I thought this research was "genetics." It wasn't until much later, and a few wrong paths, that I discovered "systematics" and "population genetics" differ from classical genetics.

When it was time for college, I applied to the University of Utah because in-state schools were what our family could afford. Luckily for me, the University of Utah was well known for its genetics programs. I had taken many advanced placement classes in high school and started college with an "honors-at-entrance" scholarship and enough credit to start as a junior. I outranked the college student that helped me pick classes during registration, and not knowing any better, I followed his advice and took organic chemistry my first semester. That was not a wise move. I failed organic chemistry and lost my scholarship. I did not appreciate the circumstance at the moment; in hindsight, however, it was good for me. Scientists must learn to cope with failure, and this was a really good start.

I began to focus more on the course content rather than on the grades, and I got a job in a lab so that I could pay tuition. I joined a genetics lab, led by a woman studying the transcription of bacteriophages. I did not understand what she was doing; I still don't. She gave me piles of reprints to read, but I was lost. I spent hours, days, counting Lac– white and Lac+ blue colonies. I often wished I was studying something bigger, something that at least moved and had legs (I had no idea at the time it would only be about 1 mm bigger and have 6 legs). My lack of fit was not lost on the principal investigator, and after an unfortunate chemical spill in the lab (no need to worry, it was just sodium chloride), she pronounced that I was "too stupid to be any good at science." That was another blow. However, I had stumbled into another lesson: learning what you do not want to do is just as important as learning what you want to do. I reconsidered my options. Scientific illustration, I thought, might be a better career choice for me. I left her lab and started taking art classes along with my science classes.

I started building an art portfolio. I met with the director of the local aviary and volunteered to design signs for their aging exhibits. Although he did not take my offer, he was encouraging. He even suggested that I take the new ornithology course being taught by a new professor at the university. I went home and enrolled immediately. The course was great, and the professor (Dr. Dale Clayton, who studied birds and their ectoparasites) had space in his lab for students. I joined. Ironically, the broader impact component of his new NSF-CAREER grant was to design signs for the exhibits at Tracy Aviary, and he wanted help. I was ecstatic. I ended up illustrating and researching interesting natural history tidbits (pre-internet) for each of 100 bird species at Tracy Aviary, and I got paid.

The Clayton lab was also very active in research. I joined as many projects as I could. All of the projects dealt with host-parasite interactions involving birds and their ectoparasitic feather lice. A local field project was censusing seasonal population dynamics of lice on wild-caught birds. Other projects involved experimental manipulations in captive systems. I dropped my art classes and redoubled my efforts in biology. One day I asked Dale to teach me how to prepare birds as museum skins (a technique used to create archival quality vouchers of avian specimens). An odd look passed over his face, and he disappeared into his office to make some phone calls. Two hours later, he emerged with a plan already in motion. Unbeknownst to me, he needed someone to help prepare birds during some upcoming fieldwork. So he had arranged for me to spend spring break learning how to skin birds at the Field Museum in Chicago before heading into the field 1 month later for a 6-week collecting expedition in the Philippines. I agreed to this arrangement immediately.

The fieldwork in the Philippines was very productive. Specimens from the trip included 1 new bird species and several new species of feather lice. (I had no idea there were still so many new species to discover.) In the time that lapsed between checking nets or while prepping specimens Dale and I also talked about many different research ideas and potential graduate projects. By the time I got on the plane home, I had an outline of a graduate project focused on studying competition between different species of ectoparasites. When I arrived home, I submitted a late application to graduate school and immediately started an experiment to study competition between "wing" and "body" lice co-infesting rock pigeons. The experiment worked. I found that different species of feather lice compete, and that this competition was mediated by host defense (much like Paine's classic work showing that predatory starfish mediate competition among mussels in the intertidal zone) (Bush and Malenke, 2008).

As a graduate student, I also explored factors governing host specificity. I transferred 4 species of lice among 6 different host species. I did crazy experiments to understand different factors that might influence the ability of lice to switch to novel host species. I attached lice to feathers on a high-speed fan to test whether lice might be able to remain attached to different sized birds during simulated, long flights. A few lice from this experiment were flung into my coffee, but, on the whole, I found lice to be incredibly tenacious on all sorts of feather surfaces. Thinking that feather coloration may be a defense against parasites, I even collected louse frass to determine if lice were digesting, or passing, the pigments in different colored feathers. (If someone had told me I was going to grow up and get paid to study louse shit, I would have assumed this was an insult; however, there I was, and I was happy.) In the end, I found that a match between host and parasite size determined whether lice could establish successfully on novel hosts and that this relationship was governed, in part, by the ability of the lice to escape from preening, a bird's principal means of ectoparasite defense (Bush and Clayton, 2006).

Meanwhile, I had also met, dated, and married (in quick succession) another student at the university. He was a political refugee from Iraq who had stood against Saddam Hussein and was trying to get back to medical school, having left Iraq in the middle of his medical studies. I was impressed by his backbone, his stance against oppression, and his ambition. When he got a late-season acceptance into med school in Grenada, he packed up and left for the Caribbean, and we began a long-distance relationship. Each of us traveled back and forth when graduate school and medical school allowed. We kept it going for a quite a while, but during his residency he eventually tired of the circumstances and gave me an ultimatum: stay with him or do research. Our marriage ended shortly thereafter. My graduate studies continued.

As a graduate student, I learned a lot from being a teaching assistant in different courses: ecology and evolution, ornithology, and others. One year I was asked to TA (be the teacher's assistant for) the "Plant Systematics" course. When I asked about this odd assignment, as I had no real background in plants or systematics, the instructor told me that I was selected because I was the only student with *any* related experience (I had once taken "Botanical Illustration"). Throughout the course I learned a lot about flowering plants and trees (phylogenetic and otherwise). I learned that you do not really understand material until you explain it to others, and I learned that nothing focuses the mind like the panic of teaching material you have just learned to a horde of critical students. I learned that you only have to be a few lessons ahead of the students, but if you do not know the answer, do *not* try to hide it. It is always better to admit what you do not know. The more I teach, the more I am convinced that this "I do not know" lesson is incredibly important. It may even be the most important lesson that we teach our students. As a society, we have trained people to memorize facts, but we have spent much less time on training people when to recognize the absence of data, or how to recognize when data are not reliable. To train the next generation of parasitologists, we need to help students recognize when an answer to a question is both unknown and interesting.

After I got my Ph.D., I became a postdoc at the University of Kansas, Natural History Museum and Biodiversity Institute. I began working with Dr. A. Townsend Peterson, who was leading a National Science Foundation Biotic Surveys and Inventories project in China. It was a 5-year project, and each year 2 ornithologists, 2 mammologists, 2 herpetologists, and 2 parasitologists were to travel to the tropical region of southern China, a region considered a global biodiversity hotspot (Myers et al., 2000), to sample terrestrial vertebrates and their parasites. I was hired to coordinate the parasite collection efforts.

At this point I felt fairly comfortable collecting ectoparasitic arthropods, but this is only a small part of what I was supposed to do. I leaned on the members of ASP. Although I had been a member of ASP for some time, this is when I felt I was fully initiated. Dr. Scott Gardner invited me to the Manter Lab, where Dr. F. Agustín Jiménez gave me a whirlwind introduction to the collection of helminths. It quickly became apparent, however, that a few days of training, even in the Manter Lab, is no way to launch an expedition and get top-quality helminths. We decided someone with real helminth experience needed to be on the expedition. For some crazy reason, Dr. Donald Duszynski agreed. After a few phone calls, and assembling a huge pile of supplies, we headed into the field with our trusty companions. Thus began my first full-immersion experience in helminthology. There was no easing into it, because a particular challenge of working in a group like this was that the ornithologists get up at dawn, catch birds until dusk, and prep late into the night. The mammologists and herpetologists do the opposite. The diversity of hosts that came through the base camp was amazing, and it kept us parasitologists very busy. Don and I settled into a schedule with very long hours, and Don patiently guided me through the dissection and preparation of hundreds of specimens of many different species.

Over the 5-year project we sampled more than 2,000 host individuals of over 350 host species. From these hosts we collected ectoparasites, endoparasites, and blood parasites. This is, of course, too much diversity for any one person to study. Back in the states, these specimens were quickly distributed to more than a dozen institutions with specialists willing to work on these different taxa (many of whom were ASP members). One particularly helpful person among this cast of characters was Dr. Vasyl Tkach. I sent Vasyl some worms that I had prepared, and he called to let me know what "could have been done better." In a very supportive way, he gave some great pointers, significantly simplified the field protocols, and even participated in a few later trips himself. I admit that preparing helminths is truly an art form that I have not yet mastered, but Vasyl is always around with encouragement and helpful tips.

On the personal front, I found that life is what happens while you are busy studying parasites. Dale Clayton and I decided to (in Dale's words): "expand our collaboration." I am delighted to say that this expanded collaboration has worked quite successfully on both the personal and professional fronts. In 2008, Dale addressed this audience as he gave a speech accepting the Ward Medal (Clayton, 2008), and we are now the first married couple to have both received Ward Medals from ASP. Unfortunately, I missed Dale's Ward Medal address because I was home with our twins, who were just days old at the time of his speech. I can, however, give an update. As Dale predicted in 2008, we have indeed packed our kids off to remote field locations, and they have actually contributed to work in Utah, Slovakia, and the Bahamas (soon they will even be co-authors on their first papers). Sonora is quite adept at removing birds from nets and identifying lice (although she often proclaims that beetles, weevils in particular, are much more interesting than lice). Austin prefers the study of bird behavior. It is not all work, though; we do manage to slip in a few extracurricular activities, like snorkeling, around periods of data collection in remote Caribbean field sites. It is a different form of work-life balance than most achieve, but it is wonderful to work so closely with family, especially a spouse who understands the stressful moments, appreciates the importance of research, and can share the joy (and occasional misery) of field work.

I joined the faculty of the University of Utah in 2010 and have continued collaborating with Dale on many new projects. Along with another long-time collaborator, Dr. Kevin Johnson, we wrote a book summarizing decades of research on the bird-louse system, placing it in the broad context of co-evolutionary research on other systems (Clayton et al., 2015). We anticipated that it would take a year (or 2) to write. Fortunately, NSF's OPUS program, which funded the writing process, did not mind when our book came out 5 years later. The 3 authors are all still talking to one other, and we have new ongoing projects.

In addition to these 2 colleagues, I have many other colleagues whom I have not yet mentioned, and they are too numerous to list here. These collaborators and friends are incredibly important, and not just because of the expertise they bring to any given project. The roller coaster of a faculty position is similar to that of graduate school, but with higher highs and lower lows. There is more mundane paperwork, and other issues constantly loom on the sidelines threatening to distract you from research. All of this is so much easier if you have others to encourage you through grant and paper rejections, celebrate awards, or otherwise distract you with their exciting discoveries and projects. I have been lucky enough to find kindred spirits in ASP and elsewhere. To all of you, thank you for encouraging messages and letters of support and for talking about science over the years.

Finally, as a faculty member I have also learned that nothing can make research more fun and rewarding than having a lab full of passionate people. I have been fortunate in having mentored such a group of students and postdocs. I have, of course, made mistakes in mentorship, and I thank each of these people for having weathered the process of working with me. I am very proud of their accomplishments, and I am grateful for the chance to work with them. I cannot tell you about all of their successes, but I will highlight 2 of their stories here.

Dr. Daniel Gustafsson was my first postdoc. He joined the lab in 2012 to work on the revision of a rather large genus of lice that no one had been crazy enough to tackle. In collaboration with Kevin Johnson and others, we took a genetically informed approach to species delineation, which made it much easier to identify phylogenetically informative morphological characters. After many years of work, we published a rather large phylogeny of the group (Bush et al., 2016) and, shortly thereafter, a monograph dividing the genus *Brueelia* into a complex consisting of more than 30 genera and over 420 species (Gustafsson and Bush, 2017). I knew we were a little crazy for tackling this project, but it was not until the 400+ page monograph was published that I fully realized that Daniel is wonderfully insane. We have now worked on 3 major projects together and have co-authored 22 papers, and, to my delight, there is no indication that this collaboration is slowing down. Daniel is now a research professor in China, and the next project is just getting started. I dearly miss walking into the lab and talking about lice and the natural history of any random organism with him on a daily basis.

Another recent project that I am particularly excited about concerns the experimental adaptive radiation of parasites. This project was made possible by many collaborators and the hard work of Scott Villa, a Ph.D. student (and later a postdoc) in the lab. One main aspect of this research was to transfer lice to different colored hosts (experimentally simulating a host switch) in order to see if lice on novel hosts would evolve cryptic coloration in the face of host defense. We found that lice rapidly adapted to life on these different colored hosts. In as little as 6 months (ca. 8 louse generations) we saw significant differences in louse color, with lice on white birds getting lighter and vice versa. Over the 4-year experiment (ca. 60 louse generations), we saw dramatic changes in color that echoed the variation existing across the entire genus, which began diverging millions of years ago. Strikingly, when we manipulated the birds' ability to defend themselves against lice by preventing preening, we found that lice on different colored birds did not differ in color. Thus, we experimentally demonstrated the rapid evolution of cryptic coloration by natural selection, and we demonstrated that host preening is the selective agent that preferentially removes lice that are conspicuously colored on host plumage (Bush et al., 2019). What is especially satisfying about this project is that cryptically colored lice have now appeared in a few textbooks along with the classic story of the peppered moths (*Biston betularia*) as a demonstration of evolution by natural selection.

We are not done with this project yet. Working with genomic collaborators, we now have a complete and annotated genome for the louse in the study: *Columbicola columbae* (Baldwin-Brown et al., 2021). We are currently working to understand the genetic architecture of the phenotypic changes that we observed among the lice in our experimental adaptive radiation. Ultimately, the goal of this work is to integrate across the micro- and macro-evolutionary dimensions of evolution in order to understand how these beautiful parasite forms have been, and are being, evolved.

To conclude, I would like to again thank Dr. Tkach for nominating me for the Henry Baldwin Ward medal. I would like to thank those who took the time to write letters of support. I would like to thank ASP members for their help and encouragement over the years. Lastly, I would like to thank you all for taking the time to be here today.

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