



INTRODUCTION OF CHARLES D. CRISCIONE, RECIPIENT OF THE HENRY BALDWIN WARD MEDAL FOR 2023

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Fellow members of the American Society of Parasitologists (ASP) and guests, I am pleased to introduce Dr. Charles Criscione, the 2023 Henry Baldwin Ward medalist. This award recognizes a member of the Society for at least 3 years, in mid-career, who has attained a position of leadership in some avenue of parasitological research. The nomination requires supporting letters that detail the strengths and contributions of the researcher's excellence and service to ASP. In this case, I must thank Drs. Timothy Anderson, Michael Blouin, and Steven Nadler (the 2013 Ward awardee) for their letters. Additional support stemmed from Drs. Cameron Goater (University of Lethbridge), Jessica Light (Texas A&M University), and Benjamin Rosenthal (U.S. Department of Agriculture). From my perspective, having this prominent group of researchers in parasite population genetics, molecular ecology, and parasite ecology critically evaluate your work and then sing your praises is almost too much already. But then again, maybe a little positive reinforcement is needed when you are an academic in mid-career. Many of us are familiar with the tropes regarding the stress of pretenure life in academia. Well, it turns out that mid-career researchers also face obstacles, and therefore celebrating the exceptional is a way for our Society to inspire and provide examples of how to successfully navigate this career stage.

Charles exceeds the criteria of membership, having been a member of ASP for >25 years and having regularly attended and presented at annual meetings since 2002. He was introduced to our Society by his M.S. supervisor, the late Dr. Bill Font, who was a long-time member and winner of the 2012 Clark P. Read Mentor Award. We have Bill to thank for pointing out to Charles that it is much more satisfying to study the parasites of reptiles and amphibians rather than just herpetology. In preparing this introduction, I reread one that Charles copresented for Bill's mentorship award and became acutely aware of the extent to which Charles keeps Bill's legacy alive by adopting certain characteristics such as his systematic approach to research (self-described as "anal"), his use of cold calls for recruitment, and his continued support of trainees after they fledge.

However, the main reason that Charles is a Ward medalist is due to his pioneering use of population genetics to better understand the evolutionary ecology of parasitism. This research direction emerged after Bill Font suggested that Charles pursue a Ph.D. with Mike Blouin at Oregon State University. At the time, Mike was one of a handful of people working on how gene flow, genetic

drift, and population structure might be uniquely interesting to study in parasites. Charles' Ph.D. work explored factors that controlled effective sizes of, and rates of, gene flow among parasite populations. His Ph.D. work is pioneering because, at the time, there were few studies using data from molecular markers to test oft-proposed hypotheses in parasite evolutionary ecology. For example, his paper on the influence of life cycle variation in salmon trematodes was one of three that demonstrated that host movement was a major determinant in parasite gene flow. His time at Oregon State University was extremely productive, with 12 papers stemming from his thesis and side projects in a range of high-impact and broadly read journals and earned him early career recognition from this Society, the Ashton Cuckler New Investigator Award. The citations for his work indicate that these papers remain influential in the field. He built upon this body of research with his postdoctoral supervisor, Tim Anderson, at the Texas Biomedical Research Institute, working to improve our understanding of the epidemiology of parasites with medical and veterinary importance such as *Ascaris* and *Schistosoma*. Once again, he ventured into new frontiers by pioneering the application of landscape genetics to parasite epidemiology and developing a genetic map to improve genomic assembly.

Upon starting his own laboratory at Texas A&M University, Charles solidified his leadership status in parasite population genetics. He returned to his roots by working on various parasites (tape-worms, trematodes, pentastomes) of different hosts including his beloved reptiles as well as embarking on a new collaboration with Bill Font on life cycle evolution. He has been awarded >\$1.6 million in grants, with continuous funding from the National Science Foundation since 2012 and has steadily published the results as well as highly cited synthetic reviews in over 30 publications in parasitology journals (e.g., our Society's journal) as well as respected and prominent ones outside our discipline.

He also continued his trailblazing ways with new explorations of the significance of inbreeding and kinship in parasites. As Tim Anderson said, "Charles' research unifies different viewpoints by celebrating the richness of parasite natural history and morphology, while using the power afforded by modern genomic and computational approaches to pioneer exciting new frontiers." For instance, he has developed new approaches to analyze parasite genetic data to estimate pedigrees, selfing rates, cosibling transmission, and kin-mating rates. There are few people that work in this area because of

the many challenges of obtaining field-collected samples, developing the molecular markers, and then applying and modifying population genetic analyses on the basis of aspects of parasite biology. As Steve Nadler eloquently summarized “Charles has not only established a productive and novel area of investigation, but his detailed quantitative approaches have yielded important insights into patterns of parasite evolution that have advanced the field—and at the same time raised the profile of microevolutionary studies of parasites among biologists.” As a result, Charles is regularly approached to collaborate on projects involving some of the coolest parasites and evolutionary questions. Who else other than Charles would uncover provocative evidence of kin selection and altruism in the zombie ant trematode, *Dicrocoelium dendriticum*! Perhaps Cam Goater said it best: “Charles is a world leader in a field where there simply aren’t many leaders. I contend that there are not many leaders because the key questions, the key theory, the key methods—are exceedingly complex. Very, very few researchers that I know have the chops to tackle these fundamental questions. We are exceedingly fortunate to have Charles in our field and we are exceedingly fortunate to have him as such a committed member of ASP.”

Indeed, Charles has been an exemplary member of the ASP. He has served on at least 9 committees (several of them elected

positions) and has been an Associate Editor for the *Journal of Parasitology*. Charles also frequently attends and presents at the national meetings of the ASP along with his lab members. I think this is notable, as beyond Bill Font, his research supervisors do not have strong relationships with ASP, and yet, Charles kept participating and shaping aspects of our Society. More recently, Charles planned the first in-person meeting following the coronavirus pandemic and even though it was held in College Station, Texas in July, the meeting was an absolute success, complete with hallmarks of Charles’ leadership including his attention to detail, financial frugality, and ability to assemble and maintain a strong, cohesive team. This year, he continues his generosity by donating his honorarium for this award to the Student Travel Fund.

I personally had the privilege of working with Charles for several years as a postdoctoral researcher. As you may be expecting by now, this opportunity began with a cold call à la Bill Font. I will never forget how thrilled and excited I was at the opportunity to work with him as I had admired his research and was certain that I would get world-class training in parasite population genetics. Working with Charles also educated me in many other aspects such as how to set up my laboratory, navigate pretenure stresses with a young family, and appreciate how Renaissance festivals can improve work–life balance. L’rds and ladies, prithee joineth me in welcoming Charles Criscione to the stage.



ACCEPTANCE OF THE 2023 HENRY BALDWIN WARD MEDAL: PEDIGREE OF A PARASITOLOGIST PROGENY

Charles D. Criscione

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When you have a sense of the history around an award, being named as a recipient makes it that much more special.—Dr. Marilyn E. Scott, “Acceptance of the Henry Baldwin Ward Medal” (Scott, 1991).

The sentiment of history is one that resonates with me and one that I wish to share with you today. Nevertheless, I wish to make it broader than the history around the award itself. It is the sense of history of the events, ideas, and people in my lifetime and those before me that make receiving the Henry Baldwin Ward Medal that much more special. So, please allow me to rephrase to make this a bit more existential: “When one has a sense of history around oneself, one marvels at how one came to be.” This statement can be interpreted in various ways, and you are free to do so. For example, it can be viewed from the perspective of someone overcoming internal or external barriers or hardship circumstances to arrive where he or she is today. However, what I am personally referring to are those “serendipitous” events that determine one’s own existence in academia (or any other profession). The events are serendipitous because they are good outcomes and, for a lack of better words, the result of chance in the sense that you did not really have any role in making them happen and it is not fate. Past Ward Medalists have used “serendipity” to describe events in their careers as well (e.g., Caira, 1998; Jensen, 2014).

I had no intention of studying parasites. Upon finishing my B.S. in zoology in 1995 from Louisiana State University (LSU), I applied to graduate programs to work on reptile, amphibian, or mammal conservation. In short, I was naive to the process and had not been accepted to these programs. The following year, while working as a keeper at the Baton Rouge Zoo, I applied and interviewed to do graduate work with a herpetologist at Southeastern Louisiana University. I ended up going to Southeastern for my M.S. (1997–2000), but not for the original intent. One night, while playing a computer game, I got a phone call from Dr. William Font (Bill). He said he was looking for a student and that the herpetologist had taken another student. Our conversation went something like this:

Bill: “Would you like to come work on parasites with me?”

Charles: “Parasi . . . what? I want to work on herps.”

Bill: “Well . . . herps have parasites!”

Charles: “Touché!!!”



Bill: “Plus, I need help in Hawai’i”

Charles: “Sounds like we have an agreement” (what I was thinking [in jest] was, “Why didn’t he mention Hawai’i in the first place?”)

This was one of those serendipitous events that clearly shaped where I am today. Why did Bill call me out of the blue? I cannot remember if I visited with him directly during my visit, but I am pretty sure I did not impress my future academic sister, Michelle Steinauer. When I met with her on my visit, she was describing her fascination with parasites, and I remarked how I did not like looking at things under a microscope. Needless to say, Bill took a chance on me. So, I must ask the existential question, “if Bill had not interrupted my computer gaming time, would I be standing here before you today?” My decision at the time was to join Bill’s

lab to learn the ropes of academia during my M.S. and then find a Ph.D. program in herpetology later on. Well, in a strange sort of way that is what happened, but not with the outcome initially sought.

Through a second serendipitous event, I ended up in my Ph.D. program with Dr. Michael Blouin (Mike) at Oregon State University (2000–2005). Mike was a quantitative and population geneticist whose lab currently worked on amphibian conservation. But, as a postdoc, Mike had ventured into the world of parasitology and made significant contributions to bring population genetics to the field of parasitology in the mid-1990s. I went to work with Mike to study parasites, not herps.

In the spring of 1998, Bill was invited to give a talk at the Ecology of Fish Parasites workshop for the British Society of Parasitology (Lewis, 1998). At this meeting, Mike gave a talk at a separate workshop entitled Nematode Population Genetics (Lewis, 1998). I do not remember exactly the timing of events, but at some point, Bill shared with me his interactions with Mike at the meeting and gave me some of Mike's papers on parasite population genetics. Around this time, I was reading up on the fields of population biology and evolutionary ecology, often stimulated via my educational experiences at Southeastern. Did Bill know this? Maybe I told Bill, and he followed up, like an advisor should, to present me with cryptic direction. Regardless, what if Bill was never invited to that meeting? What if Mike was never invited to that meeting? What if they never conversed at that meeting because their fields of study were different? Would I be here today?

My M.S. and Ph.D. were initiated with these within-lifetime serendipitous events. But let's make this even more of a "what if"—what series of serendipitous events led to the academic existence of both Bill and Mike, and hence, myself? I will address this from the broader perspective of my academic pedigree and not their personal histories per se. At first glance, following this pedigree might seem a bit off the beaten path of traditional Ward Medal presentations, which have largely focused on the within-lifetime events surrounding awardees. But I again pose the question, would I be here if not for this history? Therefore, I feel a certain obligation to acknowledge this history. Moreover, in taking this journey back in time, I learned more about the origins of my own disciplines of study: parasitology and population genetics. With this new perspective, I wonder if the very nature of the questions I study would have come about if not for this history.

Before I proceed, I need to acknowledge that much of the starting information in my pedigree came from the website the Academic Family Tree (<https://academicfamilytree.org/>). It is a non-profit volunteer driven website where you can add connections or correct mistakes. If this sort of thing interests you, I encourage you to add your parasitology family. For both my M.S. and Ph.D., I have verified my lineages going back from Mike and Bill via theses, dissertations, or other sources (these data are available upon request).

I am directly descended from Henry Baldwin Ward (Suppl. Data, Fig. S1). Ward, of course, founded *The Journal of Parasitology* in 1914, was a key contributor in founding the American Society of Parasitologists (ASP) in 1924, and served as ASP's first president (Esch et al., 2014). I earned my M.S. under Bill in 2000 at Southeastern. Bill obtained his M.S. (1972) and Ph.D. (1975) at LSU with Kenneth C. Corkum—Corkum a M.S. (1960) and Ph.D. (1963) at LSU with Harry Jackson Bennett, Bennett a M.S. (1928) and Ph.D. (1934) from University of Illinois Urbana-Champaign (UIUC). In Bill's In Memoriam (Criscione et al., 2023), I incorrectly stated that both of Bennett's degrees were

under Ward. Although this is true for his M.S., the signature on his Ph.D. is Harley Jones Van Cleave, because of Ward's retirement in 1933. Van Cleave, though, got his Ph.D. in 1913 with Ward at UIUC. This makes Ward my great-great-great academic grandfather on my M.S. side.

The handful of biographical pieces I could find on Ward briefly mentioned how his time working with Rudolph Leuckart (akin to a research assistantship) at the University of Leipzig (UL) in Germany was influential in Ward establishing a research program in parasitology in the United States. Leuckart, of course, is credited for his foundational contributions to the field of parasitology in Europe. Although these publications mentioned that Ward obtained his Ph.D. in 1892 at Harvard, there was no mention of his advisor Edward Laurens Mark or his doctoral lab environment. I do not have time/space to cover everyone in the pedigree in detail, but Mark is one to highlight. Mark was a significant figure in American biology, making early contributions to invertebrate cell and developmental biology. He is also credited with developing the "Harvard System" of in-text citation (<http://www.nasonline.org/member-directory/deceased-members/20001644.html>).

In 1903 the *Mark Anniversary Volume*, for which Ward served on the executive committee, was published celebrating Mark's 25th anniversary at Harvard (Parker, 1903). In that same year, Mark was elected to National Academy of Sciences (NAS). The volume listed 139 former students (I think grad and undergrad) including the U.S. President Theodore Roosevelt, expressing gratitude to Mark's mentorship. In addition to Ward's description of botfly development, some noteworthy contributors to this volume included William Ernest Castle (Ph.D. 1895; NAS 1915) and Herbert Spencer Jennings (Ph.D. 1896). These 2 individuals were graduate students of Mark and thus, academic brothers of Ward! Why do I mention Ward's academic brothers?

James Crow, a renowned population geneticist, wrote a history piece on the origins of population genetics (Crow, 1987a). Both Castle and Jennings are listed as early theoreticians: Castle used what we refer to as Hardy–Weinberg law for special cases prior to Hardy's and Weinberg's publications (Crow, 1999), and Jennings did early work with inbreeding, including the reduction in heterozygosity with sib-mating as well as the rate of decay in gametic disequilibrium (Crow, 1987b). Why is their work and population genetics important? Recall, it was in 1900 that Mendel's work resurfaced, but it was not yet synthesized with Darwin's evolutionary mechanism of natural selection (Crow, 1987a). Many of us are familiar with Dobzhansky's quote "Nothing in biology makes sense except in the light of evolution" (see Bromham, 2009), but today's understanding of evolution took form from about 1920 to 1950 via the population genetics theory largely developed by Sewall Wright, Ronald Fisher, and J.B.S. Haldane (Crow, 1987a). In this perspective, I like the quote of the renowned evolutionary theoretician Mike Lynch, "Nothing in evolution makes sense except in the light of population genetics" (see Bromham, 2009). So, at the turn of the 19th century while Ward was establishing parasitology as a discipline in the United States, his academic brothers, Castle and Jennings, were seeding the mathematical side of genetics and early evolutionary biology. Hence, both of my study disciplines, parasitology and population genetics, had their American origins not only around the same time frame, but also from the same academic family!

Earlier I mentioned Sewall Wright as 1 of the 3 primary figures responsible for the origination of the field of population genetics, and hence, the melding of Mendelian genetics with Darwin's theory. Thus, it would be remiss of me if I did not mention he was my great-great granduncle who did his M.S. and published his first paper on the morphology of a trematode with Ward (Wright, 1912). In Provine's biography of Wright, he notes "Wright greatly enjoyed this research" (Provine, 1986). Provine goes on to explain that Castle, who was at Harvard, came to give a lecture on his selection experiments at UIUC. Wright was fascinated with this work and inquired to work with Castle. Wright got his Ph.D. in 1915 under Castle. Ward even wrote him a congratulatory letter upon receiving a copy of Wright's dissertation (see Provine, 1986). The parallel in this serendipitous event to that of the interaction of Bill and Mike in my own academic path just seems too similar. Also, Ward's letter showed he continued to support Wright's career after his M.S.—not unlike what Bill had done for me. I wonder if Ward invited Castle to give a talk, as they were academic brothers? Did Ward arrange a meeting between the 2? What if this event never took place? Would Wright have been a parasitologist, and what then of the field of population genetics? In the end, I am here today both in terms of my fields of study, but also the direct academic lineage training of individuals that came out of the dynamic and impactful lab of Mark at the turn of the 19th century.

Interestingly, Mark obtained his Ph.D. in 1876 with Leuckart at UL. At this point with Leuckart, let me take a turn back to the present. For the sake of time and space, I will do this in the style of the Old Testament (Fig. S1). Leuckart begat Charles Otis Whitman (Ph.D. 1878, NAS 1895), who begat Charles Christopher Adams (Ph.D. 1908), who begat Alexander Grant Ruthven (Ph.D. 1906), who begat Charles D. Walker (Ph.D. 1935), who begat Henry Miles Wilbur (Ph.D. 1971), who begat Joseph A. Travis (Ph.D. 1980), who begat Michael Scott Blouin (Ph.D. 1989), who begat me (Ph.D. 2005). In my publication, "History of microevolutionary thought in parasitology" (Criscione, 2016), I joked "if only I could trace either of my other advisors' lineages back to Wright, then I could calculate my own academic inbreeding coefficient!" Well, it did not go through Wright, but rather Leuckart. If we assume 50% of scientific knowledge is passed from advisor to student (in jest to my own students, I hope it is not less!), then my $F_{\text{academic}} = (1/2)^{14}$. I wish I could spend more time, as there are very influential people in this lineage including well-known herpetologists, evolutionary ecologists, and individuals like Adams and Ruthven that had major impacts in establishing natural history museums in the United States.

I have covered my training from my M.S. and Ph.D., but I also did a postdoc (2005–2008) with Dr. Timothy J. C. Anderson (Tim) at what is now called the Texas Biomedical Research Institute (previously Southwest Foundation for Biomedical Research). Along with Mike, Tim also had significant contributions that integrated parasitology and population genetics in the mid-1990s. During my postdoc, I continued doing population genetics of parasites under the applied name of molecular epidemiology, but also picked up knowledge in linkage mapping, a classical genetic method. I did not have time to verify all my links via Tim's lineage from the Academic Family Tree, nor do I have time/space to cover them all. Nonetheless, there are some other very influential figures in ecology and evolution in this lineage as well, especially if I incorporate research assistantships as part of academic training (Fig. S1). First, I highlight I am inbred from Mike's and

Tim's lineages via Louis Agassiz, a founding member of the NAS. Going back from Tim, I have academic ancestors such as Robert Helmer MacArthur, a major driver of theoretical ecology, George Evelyn Hutchinson, who some refer to as the "father of modern ecology," and to my surprise Charles Robert Darwin himself! Huh . . . what if Darwin never got on the *Beagle*? More broadly, what if any of the connections in my academic pedigree did not happen (Suppl. Fig. S1)? Would I be here today? To me, having this sense of history makes my career and this award feel even more special.

This feeling comes from self-reflection of my own place in this history and the research contributions I have made and continue to make. In particular, integrating population genetics and parasitology has been rewarding in revealing previously intractable parasite population biology as well as elucidating how an organism's ecology relates to its evolution.

Despite the common academic-family origins of parasitology and population genetics in America, the fields did not intersect for most of the 20th century. In the history piece I wrote on the integration of microevolutionary thought in parasitology (Criscione, 2016), I noted that the first papers conducting population genetics on helminths did not come about until 1977, 46 yr ago. Using my own reference database (not scientifically unbiased), I estimate, roughly, that only about 20% of parasite population genetic studies were conducted in the first 23 yr since 1977 and 80% in the last 23 yr, since 2000. In large part, this is because molecular markers, allozymes in particular, used to study population genetics did not emerge until 1966. And really, the advent of PCR coupled with Sanger sequencing and microsatellite genotyping made population genetics of parasites more tractable. So, where do I fit in all this?

It was during my Ph.D. that I adopted a molecular ecology approach to studying parasite population biology. But, let me back up to my M.S. to understand how I ended up on this research path. My M.S. work was a survey of gecko helminth parasites. My learning curve was rapid at Southeastern and I owe much of my career to the Southeastern faculty and the scientific rigor of their program. During this time, I learned parasitological techniques, systematics and phylogenetics, ecological principles, and statistical analyses. In doing this work, I had to rely on morphology, a necessary tool and basis for many ecological or evolutionary studies. I must admit that phenotypic variation in morphology did lead to frustration in species identification, but it also generated many interesting questions at the interface with population biology. Was the variation investigator induced via fixation methods? Was it ecologically driven by density dependence (a.k.a. crowding; Criscione and Font, 2001)? Was it induced by host environment? Where there multiple species? And if so, how much phenotypic difference is needed to delimit a species, or what do you do if trait variation overlaps between presumed species?

The questions I became interested in were difficult because there are hurdles in studying parasite population biology such as small body sizes, sites of infection, unknown biodiversity (including cryptic species), and labor-intense lab maintenance. These factors can impede or preclude direct observations or experimentation on important population biology topics like mating behaviors, dispersal across landscapes, and transmission among hosts. Do not get me wrong, there are some of you that do these things, and it is remarkable! I was just interested in trying to find an alternative means, especially for systems we cannot bring into the

lab, and to elucidate patterns in nature. What I became fascinated with upon reading Mike's papers as well as Steve Nadler's paper (Nadler, 1995) was the potential for what molecular markers could help us address about parasite population biology in nature and hence, better understand their evolution.

Out of all of this emerged what has largely been the theme of my research since my Ph.D., which is understanding the interplay between an organism's ecology and its evolution. The 2 primary broad-based questions I address are (1) what can population genetics methods or patterns tell us about parasite biology in the field, and (2) what ecological and life history traits of parasites influence their evolutionary mechanisms? Armed with the parasite ecology knowledge I gained during my M.S., I became interested in relating classical ecological topics in parasitology to parasite evolution. During my doctoral studies and postdoc, I began to integrate these parasitological concepts with population genetics.

The following are a few examples. We translated the community ecology concept of how autogenic vs. allogenic life cycles influence parasite communities among watersheds down to the intraspecific level to understand how life cycles might affect gene flow. Parasite community structure has been used to identify fish stocks. We demonstrated how genetic assignment tests of a parasite can be used in the same way. We addressed the role of intrapopulations in shaping effective population size, a key population genetics parameter that quantifies the rate of genetic drift. We used population genetics to elucidate foci of transmission independent of relying on infection intensities, which do not tell about source of infection. We did the first linkage map for a helminth. This was particularly fun because it was cool to see first-hand Mendel's principles of segregation and independent assortment. It is with this integrated background of ecological parasitology and population genetics that I started my own lab at Texas A&M University in 2008.

At this point, I need to take a step back into history again and give some quotes from the 1969 Ward Medal acceptance speech of Franklin Sogandares-Bernal (Sogandares-Bernal, 1970).

One of the biggest gaps in our knowledge of parasitism is in the general area of genetics. It is seldom studied because of the "complexity" of the systems. Early in my studies of hermaphroditic Digenea I became perturbed by the fact that from a genetic point view we were no closer to really understanding the mode of inheritance of these worms than was Arthur Looss at the turn of the [19th] century. Because these worms are hermaphroditic it was assumed, a priori, by many investigators, that they were self-mating . . . The fact remains, however, that very basic questions relating to the contributions of self- or cross-matings to the species population structure in nature are to this day unanswered.

I must admit I had not read his speech until May of this year. I am familiar with a few papers that came out of his lab dealing with parasitic flatworm mating systems, but clearly the topic was of major interest to his lab at the time. Unfortunately, the genetic tools to conduct such studies were just being developed and it looks like he went in a different direction for his research program. If I had not read his acceptance speech, someone might have accused me of plagiarizing him because I likely would have had similar statements. Now, I can just use his quotes. The point is that several recent studies from my lab have begun to tackle

hermaphroditic mating systems of parasitic flatworms. In particular, using genotype data along with metrics we developed, we are now able to use field-collected specimens to elucidate hermaphroditic parasite mating biology in nature.

The success in my lab is because of the hard work and inquisitiveness of my excellent academic progeny. My 2 former postdocs (Dr. Jillian Detwiler and Dr. Isabel Caballero) were instrumental in various gecko-tapeworm projects looking at parasite mating systems and inbreeding depression. We conducted studies to examine how the distribution of infection intensities (an emergent property of transmission) can impact selfing rates, as well as how who you are transmitted with, in terms of relatedness, can impact kin-mating. I'll mention a few cool things on this research. First, I returned to a system from my M.S. work. I never foresaw this as a M.S. student. Second, our data were based on field-collected samples and thus, represent the first elucidation of a flatworm parasite primary mating system in nature. For some perspective, a review in 2005 had primary mating system data from over 350 plant species (Goodwillie et al., 2005); our paper was in 2017 (Detwiler et al., 2017). Third, these studies incorporated the parasite-centric ecological dynamics of infrapopulations, infection intensities, crowding, and transmission to illustrate how they play a role in shaping parasite evolution. Specifically, these ecological facets shape the mating system, which in turn shapes the evolutionary mechanism of inbreeding.

Andrew Sakla was a M.S. student that conducted morphological work on pentastomes showing likely host induced variation in an introduced parasite species that jumped from introduced geckos into native green anoles. I had 2 international visiting student scientists in my lab. Dr. Isabel Valdivia studied the mating system of a marine trematode with a precocious life cycle and Dr. Sirilak Dusitsittipon studied lineage diversity and found incorrect species identifications in relation to data-based sequence data in the rat lungworm *Angiostrongylus cantonensis*. My former Ph.D. student, Dr. Mary Janecka, conducted a conservation genetics study on a delisted water snake. In conjunction, she sampled trematodes from the mouths of water snakes in this river system. She will soon have some papers coming out on how dendritic river systems influence parasite distributions across the drainage and parasite population genetic structure.

My lab has primarily been funded from 2 NSF grants (DEB 1145508, DEB 1655147) focusing on the evolutionary patterns and population genetic consequences of changes in life cycle complexity. This work has used the trematode genus *Alloglossidium* as its focus and has taken us across the southern and midwestern United States sampling catfishes, crayfishes, and leeches. The origins of this work stem from Bill's past work in this genus and a conversation I had with him early in my doctoral work. I was looking for systems to contrast the population genetics of parasites with different life cycles. We discussed this system, but at the time, it was not ideal as I was in the Pacific Northwest, so sampling would have been difficult. However, I banked the system. In Texas, it became feasible for me to study this system.

The genus has been of interest to parasitologists because of the fascinating life cycle variation found among the species. An interesting quote from my great-great academic grandfather on my M.S. side, Harley Van Cleave, shows that phenotypic variation stifled him as well. "More than five hundred specimens of *Alloglossidium* are in our fish parasite collection. An intensive study of this material has left us somewhat in doubt as to the actual

number of species represented. Since most of the variable characters are integrading, we recognize but two species as set forth in the foregoing key” (Van Cleave and Mueller, 1934). Indeed today with molecular data, we recognize more than just 2 species of *Alloglossidium* from ictalurid fishes (Kasl et al., 2018).

My former Ph.D. student, Dr. Emily Kasl, carried out much of our early survey work and produced the molecular phylogeny of the genus to elucidate the evolutionary transitions of the different life cycle patterns (Kasl et al., 2018). The genus is also an ideal system to look at the interplay between the ecology of these life cycle patterns and downstream evolutionary consequences. Among the facultative precocious populations of *Alloglossidium progeneticum*, the forced self-mating when maturing in their cysts should favor devoting more resources to female function. Emily tested and confirmed a reduction in male sex allocation among the facultative precocious populations compared to the obligate 3-host populations. At this meeting, my current Ph.D. student, Jenna Hulke, gave a presentation that confirmed the high selfing rates in the facultative precocious populations and that the obligate 3-host populations are largely in Hardy–Weinberg equilibrium.

I currently have 3 excellent Ph.D. students. A few weeks back when I was working on my speech, Jenna came into my office and I was showing her some of my academic pedigree. She gleefully inquired, “does this mean you are going to add my connection under your name?” Wearing my academic father hat, I sarcastically replied, “as soon as you get your Ph.D. I will put your name there.” I do wish to highlight that all 3 of my current students have pedigrees tracing to ASP members. In addition, to emphasize the importance of Tami’s presidential speech at this year’s meeting (Cook, 2023), all came from primarily undergraduate institutions. Jenna can be traced back to Dr. Armand Kuris via Todd Huspeni at University of Wisconsin–Stevens Point, Ryne to Dr. Julian Hill-ryer via Lisa Brown at Georgia Southern University, and Chelsea to our current ASP President, Tami Cook at Sam Houston State University. These 3 are taking my lab, I hope (said in jest), into the population genomics age, where I believe the technologies are now becoming more accessible to truly non-model species.

Jenna will be done in another year and will have some very impactful papers coming out on various population genetics studies on species in the genus *Alloglossidium* dealing with consequences in complex life cycle changes. We also have planned some comparative population genomics with the genus to address how organismal life history traits influence genome evolution itself. Ryne is using our gecko–helminth system to venture to the “dark side” to examine host–helminth interactions from the host point of view. Knowledge of reptile immunology in relation to helminth infections is next to non-existent. We are venturing into brave new territory and will be using genomics and population genomics to look at major histocompatibility complex evolution under natural infections. Chelsea is staying on the “light side” to look at the genomics of our favorite tapeworm *Oochoristica javaensis*. We hope to use this system to explore the population genomics of an invasive and a mixed-mating species as well as conduct some comparative genomics of mammalian and reptilian cyclophyllidiean tapeworms.

If I were to summarize what I think is the significance of my work, it is that I try to look at evolution from the perspective of the parasite. I feel there is often a host-centric view of parasite evolution, in part because such emphasis is often given to parasites in relation to human or animal health. By bringing parasite-centric

ecological concepts into the picture of some common fields of study in evolutionary biology (e.g., hermaphroditic mating systems), some simple but fascinating things emerge both for the elucidation of the parasites themselves, but also evolutionary biology in general. To illustrate, I would like to describe 2 quick examples.

The first stemmed from our tapeworm mating system work, where we examined the relationship of intensity of infection to selfing rate (Detwiler et al., 2017). Because endoparasites exist in infra-populations, these are closed mating systems (i.e., cannot mate with parasites in another host) that we can use to our advantage. As a null model, if there is random mating within hosts, then there is an inverse power relationship between the selfing rate and infection intensity (e.g., an intensity of 2 leads to 50% selfing, 3 to 33%, 4 to 25% and so on). From this we can estimate a population level selfing rate, which can be calculated as a weighted average of the average selfing rates within hosts where the weights are the proportion of worms in a host relative to the total number of tapeworms. The latter weighting assumes random reproductive success across the parasite component population. This reduces simply to the inverse of the mean infection intensity (Detwiler et al., 2017). Stop and think about this. We use infection intensities all the time in parasite ecological studies, but have never derived this relationship that can drive an evolutionary mechanism. Not only does this relationship serve as a null, but we can use this to ask if mating systems are shaped by parasite demography and/or to test inbreeding depression in the field (making certain assumptions—to be published in the near future).

We can also incorporate “crowding,” another classic parasitology concept, into the picture by changing the weighting scheme. The latter is shown in some recent work that will be coming out of our lab soon. Jenna has data showing that population genetic estimates of selfing in *Alloglossidium renale* are slightly higher than that expected under the mean infection intensities as per the relationship I just described. If we incorporate crowding into the demographic selfing rate estimates, we can explain the genetic estimates of selfing rates better. Moreover, congruence in the genetic estimates and demographic estimates indicates there is no support for inbreeding depression. I emphasize that these data are from field-collected samples; hence, conclusions reflect natural circumstances. Along with prior work on the tapeworm *Oochoristica javaensis*, we now have 2 parasitic flatworms that appear to have population selfing rates influenced by the classic crowding effect.

In the second example, we extended our work from the tapeworm into the clonal dynamics of trematodes (Criscione et al., 2022). We have developed a metric that gives information both on transmission in terms of probability of co-transmitted kin (such as clonemates) and mating systems in terms of a potential kin-mating (such as clonemate-mating) rate. This metric is the proportion of kin dyads within a host. I say “developed,” but really it is a repurposing of a metric that is commonly used in community ecology (i.e., complement of Hurlbert’s [1971] probability of interspecific encounter). In population genetics, the same mathematical statistic is the complement of Nei’s gene diversity (Nei, 1987). I am not aware of another metric that is so diverse in its use. Moreover, I am not aware of another metric that gives simultaneous information on the ecology and the evolution of an organism (though there probably is). The development of this metric really came out of necessity in trying to figure out a useful way of summarizing the genotype data. Maybe I should not admit this, but when I “developed” it, I was not even aware that it was mathematically equivalent to its community

ecology counterpart. I found this out later on by tinkering with some numbers. Again, these are not complicated concepts, but the use of the infrapopulation concept and the fact that the infrapopulation represents a closed mating system to endoparasites is what brought all this to light. Revisiting Sogandares-Bernal's statement in his Ward speech 53 yr ago (Sogandares-Bernal, 1970), we have developed methods and analyzed a handful of species to elucidate hermaphroditic parasite mating systems in nature.

Thus far, I have spoken of my academic ancestors, and my own progeny, but there are many other family members that have contributed to how I came to be. I now take some time to acknowledge these people.

To my wife of 23 yr, Miranda, and my 2 sons, Anthony and Mitchell, thanks for putting up with me. I have tried and continue to try to make decisions on a family-first basis, but academia can be cruel and sometimes it is not always possible. Needless to say, y'all have been patient with me. In contrast to being a student of a field of study, nobody really teaches you how to be a husband or a parent. You just learn by being thrown into the deep end of the pool. Y'all have shaped who I am in more ways than one. I love y'all very much.

As a small aside, my family has a little history with ASP. Some of you may remember my sons from ASP in Colorado Springs in 2010. At the auction, I obtained the Bill Campbell painting Rhinebot Duo, which is now hanging in my office. Next to it, I have written the "Folklore of the Purchase" stating the following "Often paying top dollar, Dr. Janine Caira and Dr. Kirsten Jensen were common purchasers of Bill's paintings. In a strategic plan, Dr. Charles D. Criscione, with the permission of his wife, Miranda D. Mire-Criscione, had his 2 sons, Anthony and Mitchell, bid for the painting. In the end, Dr. Caira and Dr. Jensen succumbed to the cuteness and guilt of bidding against kids, thereby leading to the purchase of Dr. Criscione's prized painting."

To my large Italian family, especially my parents Sam, Sr. and Jacquelyn and my brothers Sam, Jr. and Peter, for your support in anything I have done throughout my life. I have never had anyone in my family ever tell me that I could not do something. To my wife's Cajun family, especially her father Lucien Mire and deceased mother Michelle Mire, for welcoming me into their family even though I am the strange scientist.

To my home city of New Orleans, although you are not a person, you are a spirit. I grew up in the "concrete swamp," playing ball in the streets, eating crawfish and seafood second to none, constantly wishing the Saints would win the Super Bowl (which came true in 2010), and chasing floats and watching "bead blooms" of trees every year during Mardi Gras. You even played a role in helping me get Miranda's phone number.

To my wrestling families from my high school team to my youth coaching to watching my own 2 sons wrestle. It is a demanding sport with a love-hate relationship. In the end, it takes something special to just step on the mat. I know some other ASP members are former wrestlers, so you know what I mean.

To my immediate academic fathers: first and foremost, to Bill Font for supporting me throughout my career, educating me about parasites, your passion about science, your perfect floating buckets, and texting me during college world series games. I wish you were here today. "Hey Bill, LSU won again this year!" To Mike Blouin for your open door policy to entertain my ideas, your wisdom in correcting or refining my ideas, your continued support, and your carefree nature. I became an evolutionary

biologist under your guidance. To Tim Anderson for introducing me to classical genetics, demonstrating how to write grants and to relate one's work to non-parasite systems, your appreciation for parasite evolution, and continued support.

To my academic siblings Michelle Steinauer, Ashleigh Smythe, Ricky Fiorillo, Amanda Vincent, Eric Hoffman, Kirsten Monsen, and Jacob Tennessen for camaraderie, scientific engagement, and teaching me various things. Highlighting the intellectual environment I was exposed to over my graduate career, all of you are currently in academia or government leadership positions. To Michelle, in particular, when I was dissecting geckos once you asked me what my research question was going to be with the gecko-helminth survey. Like a big sister, you looked out for a little brother and taught me how to look into the broader biological question. Michelle is also a member of the ICOPA-6. Eric also looked out for his little brother and I am indebted to him for teaching me molecular lab methods as well as to being an ongoing colleague whenever we get the chance to meet up.

To my faculty mentors, colleagues, and friends Adam Jones and Gil Rosenthal, y'all are 2 of the most stellar evolutionary biologists I know and my career at A&M has greatly benefited from my interactions with y'all. I miss both of y'all since y'all have left A&M. To Wayne Versaw who has been a friend, mentor, and guide as I navigate the world of academic administration. To Will Bailey, the "money guy" in my department, who is always fun to joke around with—I greatly appreciate your help in managing funds and personnel over the years at A&M. To my former department head, Tom McKnight, for leaving me alone (I mean that in a good way).

To Mike Kemp who entertained me with old ASP stories when I started A&M back in 2008. Mike once gave a joke presentation in which claimed to discover the human soul via molecular biology techniques; the soul was a schistosome parasite. He actually published this joke in the *Journal of Irreproducible Results*. A quick aside, along with Mike and John "Dick" Seed, I am the third person to receive the Ward Medal who was at Texas A&M at the time (Mike received the Ward Medal in 1983 and Dick in 1976). Of the 60 Ward Medals awarded, that makes Texas A&M University have the most Ward Medalists out of any academic or governmental institution. I would have never thought that.

To Steve Nadler for being one of the other primary figures in the United States for integrating population genetics into parasitology and thus, being a source of inspiration for much of my work. To Susan Perkins, who, when I was a graduate student in 2004, came to my poster at the Evolution meetings in Fort Collins, Colorado. As you were one of the earliest parasitologists to venture into molecular ecology, you made me feel relevant at such a large meeting. I know you also supported my career behind the scenes. To Ash Bullard and Janine Caira for intimidating me at my first scientific meeting. In 1997, just after Bill asked me to join his lab, Bill took me to the Southeastern Society of Parasitologists (SSP) in Greenville, South Carolina. I went to lunch with a group including Ash and Janine and remember them speaking a mile a minute and spouting various parasite scientific names. I was amazed at their knowledge and still am today. Ash has been a continued friend at ASP and I know Janine has supported my career behind the scenes in various ways. Thanks to all 4 for the early inspiration and ongoing intellectual stimulation over the years.

To Jessica Light for being part of the ICOPA-6, and being a source of wisdom and a friend at A&M. Jessica and I were at a

social function the night I got the call from Avril about Bill's untimely death. Bill was on Jessica's doctoral committee and knew Bill well, so having Jessica there to share the sad news provided me comfort. To Cam Goater, for being a great collaborator on the lancet fluke work, a great ecologist, and for often recrafting my wording so others can understand. To Ben Rosenthal for bringing parasite population genetics to the USDA and supporting my career behind the scenes. To Ben Hanelt for our "life" conversations at ASP as well as sharing some adventures, such as seeing hairy cows in Scotland; Michelle was on that trip as well. To Derek Zelmer for being a great quantitative ecologist, but also making fun of my "see-through" gecko picture when I was a young M.S. student presenting at SSP. By the way Derek, you can also see *Alloglossidium renale* infections without dissecting grass shrimp.

To Chris Whipps, my academic half-brother (our major advisors were on each other's committees), for our many ASP adventures together. It all started with the ICOPA-6 rooming together (6 of us in a room) in Vancouver when ASP met with the International Congress of Parasitology (ICOPA) in 2002, to being groupies and making editorial changes on a sign in Halifax in 2003, to evacuating Mobile, Alabama in a less than stable state when Hurricane Dennis decided to crash our ASP party in 2005. One of the reasons I went to Oregon State University was because I saw your poster and met you at the student recruitment visit. As I was not in a parasite lab in Oregon, it was great to have someone to talk with about parasites.

To Jillian Detwiler for helping me kick start my lab at A&M and nominating me for this award. As a parent, it is an honor to have your progeny think well of you. On a visit to Purdue, I met Jillian when she was a Ph.D. student. Sometimes you just get a feeling about someone when you first meet them and know they are going to go far. That is why I picked up the phone and asked her to join my lab as a postdoc; one of the best decisions I made in my career. We are on 9 papers together and likely have a few more in the future.

To Reginald Blaylock, (the late) Robin Overstreet, Phil LoVerde, Matt Bolek, Sara Brant, Herman Eure, Kelli Sapp, John Hawdon, Kirsten Jensen, Sam Loker, Vincent Connors, Isaure de Buron, David Marcogliese, Bruce Conn, Julián Hillyer, Kristin Herrmann, Joseph Camp, Florian Reyda, Stephen Curran, Kym Jacobson, Sarah Williams-Blangero, Robert Poulin, John Gilleard, William Ardren, Román Vilas, and Thierry de Meeûs for career-stage support, various professional interactions, and/or ASP adventures over the years. To the many others that have contributed in some way to my career: co-author, reviewer, colleague, and so on, I apologize for not mentioning you, but I do recognize many others have played a role in how I came to be.

To our President, Dr. Tamara Cook, to our Editor for the *Journal of Parasitology*, Dr. Richard Clopton, to our Secretary/Treasurer Lee Couch as well as all past and future presidents, editors, and ASP committee service members and officers, I thank you for your volunteer service. Our discipline would not exist if not for your altruism and wisdom. I thank the Awards Committee for selecting me to be a Ward Medal recipient.

As I stated at the start of my speech, "It is the sense of history of the events, ideas, and people in my lifetime and those before me that make receiving the Henry Baldwin Ward Medal that much more special." In this context, I would like to conclude my acceptance of the Henry Baldwin Ward Medal by revisiting a statement given by Esch, Desser, and Nickol in a history piece

they wrote in 2014 about the *Journal of Parasitology* (Esch et al., 2014). They state, "It was said that, 'Ward was to the United States as Leuckart was to Germany.' Most parasitologists refer to Ward as the father of American parasitology. It is of interest, however, that Ward considered Joseph Leidy as the founder of American parasitology (Ward, 1923). We are not certain how much difference there is between Father and Founder!"

I know the difference and it is reflected in the title of my speech "Pedigree of a Parasitologist Progeny." Pedigrees denote familial relationships. Although Leidy had students, I am not aware that any went on in the field of parasitology (please correct me in a future publication if I am wrong). I do not know how many students Ward had, but many of us can trace our academic pedigree back to him, as he had many. Even if you cannot trace your academic lineage directly to Ward, you are still a descendent of him if you are a member of ASP. After all, he was instrumental in creating this society and the journal. The words father, mother, brother, sister, son, daughter, aunt, uncle and so on, have meaning. The meaning is simple; it is family. Although Leidy may have been the first to study parasites in America, Ward created an academic family and that family is us, The American Society of Parasitologists. It makes it all the more special to receive the Henry Baldwin Ward Medal from my ASP family. I often joke that I only wear a coat and tie at family weddings and funerals. Today is neither, but it is a special family function; it is our yearly reunion! Thank you all for the intellectual interactions, support of my career, fun social interactions, and for honoring me with this award!

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