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Interview with John C. Avise, recipient of the 2009 Alfred Russel Wallace award

by Brett R. Riddle¹

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Brett R. Riddle. Wallace is considered the “Father of Biogeography”, Darwin the “Father of Evolution”, and Linnaeus the “Father of Taxonomy”; and now you are the “Father of Phylogeography”, which admittedly is a young discipline compared to the other three. If you were to look perhaps 100 years into the future, do you have a sense that phylogeography will become a discrete discipline alongside those other three pillars in the biodiversity sciences?

John C. Avise. I'm flattered (and also a bit embarrassed) that you would even imagine placing my name in such lofty company. Nevertheless, I do believe that phylogeography has prompted a revolutionary way to look at the world, important enough to merit at least a bookmark in the history of science. Prior to phylogeography's emergence as a recognizable discipline in the mid-1980s, two dominant halves of evolutionary biology had remained quite disconnected. On the one side was population genetics, a well-established microevolutionary discipline that deals with various forces (such as natural selection and genetic drift) that can shape allelic and genotypic frequencies in conspecific populations. On the other side was phylogenetic biology, a discipline that aims to estimate historical relationships mostly of supra-specific taxa. Ever since my early days in graduate school, I perceived as incredibly ironic the fact that population genetics and phylogenetic biology had extremely little contact, despite the reality that both of these academic traditions deal ultimately with the histories of genetic lineages, albeit across different timescales.

BRR. Ironic, I agree, and phylogeography certainly has filled the role as an integrator between those disciplines.

JCA. Well, that's how I like to think of it, anyway. In my opinion, a proper reading of history will

credit phylogeography with having forged some of the earliest empirical and conceptual bridges between micro- and macro-evolutionary thought in genetics. A century from now, I suspect that phylogeography will still be recognizable as a discipline, although perhaps so thoroughly integrated into evolutionary research that most biologists will simply take for granted that an emphasis on genealogy in space offers a seamless approach for connecting the evolutionary-genetic histories of organisms below and above the level of species.

BRR. Right, and that synthesis certainly is becoming more clear all the time. In your view, has phylogeography been more successful in generating new questions and avenues of research because of that power of integration, or really as a new approach to addressing older questions?

JCA. I think it's some of both. Phylogeography is a conceptually bounteous discipline in the sense mentioned above, but it's also a data-rich field that has opened highly practical ways to address biogeographic questions, many of which had existed before but others of which (especially within species) had been formulated poorly at best. Beginning with the introduction of mitochondrial (mtDNA) data to population biology in the 1970s, geneticists finally gained empirical access to gene genealogies within as well as among species, and that's something that had not been practicable (nor even much dreamed of) prior to the phylogeographic revolution. So, phylogeography has become a spirited mix of some things old but many things new.

BRR. And how do you see the conceptual and the empirical sides of phylogeography interacting with one another to drive the field's development?

JCA. I see them as synergistic or mutually reinforcing. For example, mitochondrial data provided much of the original motivation for developing coalescent theory, but the latter in turn now stimulates ongoing efforts to gather additional genealogical information from multiple loci and species. So, I see extensive feedback between data and theory in phylogeography. Indeed, such synergism probably characterizes nearly all young and vibrant fields of science, some other examples being astrophysics and molecular biology.

BRR. Have there been any limitations or dead-ends that have surprised you, or questions that you might have seen 10-20 years ago developing but really have not come to fruition the way you might have envisioned?

JCA. Yes, definitely. For example, I'm very surprised that the field has not yet moved with much greater effectiveness into analyses and interpretations of nuclear genealogies. During its first 20 years and beyond, the field of phylogeography has been tied closely to cytoplasmic genomes because of the relatively clear genealogical signals that these non-recombining haploid segments of DNA provide. Thus, a major challenge for the field now is to extend genealogical concepts and empiricism to the nuclear genome, where the vast majority of each species' total genetic history must in principle reside.

BRR. Has that been mostly a methods constraint, or a theory constraint? Is it technological, or just that people have not figured out analytically how to deal with nuclear genomes?

JCA. The constraint is definitely technical in part. For example, one immediate logistic hurdle is how

to isolate and assay nuclear haplotypes, one at a time, from diploid tissue. There are several ways to do this in model systems, but in general the challenge has proved to be stiffer than many people probably anticipated. However, the constraint is also conceptual in part, because a multi-locus coalescent theory for structured populations will have to be developed before we can gain a clear interpretation of the multitudinous pathways that haplotypes at unlinked nuclear loci undoubtedly have traversed during a species' history. So, the challenges are both conceptual and technological. Eventually, the field of phylogeography will have to come to grips with dissecting nuclear genomes in ways that are at least somewhat analogous to how mtDNA data traditionally have been handled.

BRR. Do you see any technological thresholds on the horizon that will overcome some of those problems? Genomics based technology?

JCA. Yes. I think the field is moving gradually in several directions to address these shortcomings, and genomics-based technologies will certainly play key roles. But let me frame the situation in the following way: If I were a young researcher, just starting my career now, I would probably strive to pioneer a new approach that I might label "haplotypic genetics" or perhaps "gamete-based genetics". The basic idea, in part, would be to take full advantage of nature's own methods for purifying nuclear haplotypes. Every time a gamete is produced, nature in effect has isolated a discrete piece of DNA at each and every nuclear locus. If these could be isolated and sequenced in large numbers, a vast new category of genealogical information might be tapped and then interpreted (using a multi-locus coalescent theory) in an expanded phylogeographic framework. This

Two special issues on the 4th IBS Meeting are now out

The December 2009 issue of *EcoHealth* (<http://www.springerlink.com/content/1612-9202/6/4/>) included a special feature on the biogeography of disease, the outcome of a symposium organized by Kate Smith and Sam Schneider at the 4th IBS International Meeting (Mérida, Mexico, 2009).

Ecography published in July a special issue with a selection of contributions that arose from the Mérida meeting, representing the diversity of current biogeographical research. The issue is available at <http://www.wiley.com/bw/journal.asp?ref=0906-7590>.

would be a truly revolutionary development. Long before the phylogeographic era, much of traditional population genetics dealt with diploid genotypes, allele frequencies, and populations as units of analysis, but there wasn't the explicit genealogical perspective that a gamete-based genetics might promote. The net result could be a fresh way of thinking about the biological world that should compliment and enrich not only phylogeography but also much of traditional phylogenetics and population genetics.

BRR. Would you envision, if you just took that a little bit further, and you were thinking about a model system to start developing that sort of genetics, going straight to a diploid based system, or would you start with something simpler, something that's haploid?

JCA. If I had the necessary resources (time, personnel, and money), I would approach the problem from a variety of different angles. I might indeed start with a haploid (or perhaps a haplo-diploid) genetic system for tractability, but eventually I would want to expand the methods and concepts to diploid sexual creatures. Although certainly challenging, the whole approach should be technologically feasible, as evidenced for example by the work of Norman Arnheim at the University of Southern California, who has forged a highly successful career by applying gametic assays to questions in human population genetics. In many publications over the years, Arnheim and his colleagues have demonstrated a remarkable diversity of applications for this kind of gamete-based approach. If it can be done in humans, it surely must be do-able more generally.

BRR. Going back to phylogeography as it exists today, can you briefly think about some of the greatest successes you've seen – I think you've probably written about them before – or perhaps some of the successes that have been the most surprising to you?

JCA. I've written several review papers and books on the many unanticipated discoveries from phylogeography. Especially in the early years, when

the field was still in its infancy, it seems like my students and I encountered one big surprise after another, almost on a monthly basis. A lot of that had to do with stunning findings about mtDNA structure and evolution, but some of it had to do more broadly with genealogical patterns, processes, and principles. One example of the latter was our discovery that particular phylogeographic patterns sometimes recur across multiple co-distributed species in nature. Before then, I had supposed that nearly every species (and perhaps nearly every locus in sexual taxa) might tend to display a unique and idiosyncratic genealogical history, so I was genuinely amazed when my laboratory (and many others) began to uncover rather consistent phylogeographic themes or patterns at several levels of biological organization. This in turn led to our elaboration of "principles of genealogical concordance" that have become centerpieces of phylogeographic thought.

BRR. Does that expectation of idiosyncrasy derive from the expectation that the recent and shallow intra-specific world works differently from the deep and across-species world where, since the 1970's, people have certainly been expecting to see such recurring patterns derived from a sort of vicariance-based biogeographic perspective?

JCA. You're quite justified in suggesting that my astonishment might merely reflect my naivety or ignorance at that time. My training had been mostly in population genetics and ecology, so perhaps I would have been somewhat less surprised had I been trained instead as a vicariance biogeographer. In any event, in most cases I still prefer to deem the simplest null hypothesis as being a general paucity of extreme consistency in nature.

BRR. So what you're doing is really confirming your previous discussion about the extreme conceptual differences between the micro-evolutionary population-genetic and macro-evolutionary phylogenetic-biology worlds that had existed until then.

JCA. You make a valid point. But regardless of whether these and many other phylogeographic eye-openers about nature were discipline-wide revelations at that time or merely personal insights for me then, they are now thoroughly woven into the basic fabric of modern phylogeography.

BRR. Getting back to those early days, you talked a little at the IBS meeting in Mexico last year about the role of serendipity in your role in discovering phylogeography. What I'd like to ask is for you to talk a bit more about serendipity in terms of being in the right place at the right time and having the right molecule to work with.

JCA. In many respects, I can be thought of as the poster-child for serendipity in science. My entire career has been one fortuitous break after another. Let me give you an example. [I've written about this before, but the story bears repeating.] In the mid-1970s, I became involved with mtDNA by pure good fortune. I had just started as an Assistant Professor at the University of Georgia when I gave a departmental seminar about an allozyme project that I had conducted on fish. I concluded my talk by telling the audience that although it might be fine to study protein products of structural genes, the real stuff of evolution was probably genetic regulation. [This was at a time when Allan Wilson and others had first proposed key evolutionary roles for regulatory genes.] So, I queried the audience for any suggestions about how I might shift the focus of my research to gene regulation. One person raised his hand and asked, "Have you tried restriction enzymes?" I replied, "What are restriction enzymes?" [I honestly didn't know; they had been discovered only recently.] So, I soon read up on these proteins and learned that they are like little scissors that snip DNA at specific recognition sites. Wow, wouldn't it be great if I could harness restriction enzymes to examine repetitive nuclear

DNA, which was by then widely suspected to play some role in gene regulation? Accordingly, I approached several biochemistry professors at UGA to ask whether I could work in their lab for a few weeks to learn restriction techniques. Except for one person, they all politely said "no". The one exception was Robert Lansman, who welcomed me into his laboratory but who also lamented that he knew little about the nuclear genome, having instead devoted his career to the biochemistry of mtDNA. "What is mtDNA?", I asked. Well, I soon found out, and, as they say, "the rest is history". In Bob's lab, we soon began purifying restriction enzymes (because they weren't yet commercially available) and digesting mtDNA, which I never imagined would hold any special evolutionary interest in its own right. Of course, the mitochondrial genome turned out to have many wonderful properties that make it nearly ideal for what later would become known as phylogeographic analyses. Such studies on a wide variety of vertebrate and invertebrate animals were to become my occupation and preoccupation for the ensuing 20 years.

BRR. I'm sitting here thinking that this is loosely analogous to contingency in evolution and adaptive radiations. I don't want to take that too far, but my question would be: mitochondrial DNA really was an important part of the story of getting phylogeography off the ground to begin with, and if you had not been in Bob Lansman's laboratory at the right time, working with the right person who himself did not really know the power of this molecule in an evolutionary and biogeographic sense ...

JCA. Right, Robert was a biochemist and physiologist, so his academic background was entirely different from my training as a population geneticist and natural historian.

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BRR. Yes ... totally different view, and so have you ever thought about, had you not been there, and Bob not been there, how long, if at all, it might have taken phylogeography to develop and what it might look like today?

JCA. I've often mused about that, and I've also wondered whether a cleanly recognizable field of phylogeography would even exist today? Honestly, I rather doubt it. Although it is true, of course, that many people would still be using cytoplasmic genomes as powerful genealogical tools, it also seems unlikely to me that such approaches would inevitably have become wrapped into a broader and cohesive conceptual evolutionary framework. How the word 'phylogeography' itself was coined came about as follows. In the late 1970s, as we began writing scientific articles about the spatial distributions of matrilineal haplotypes in various species, I was forced to use cumbersome phrases to summarize a straightforward observation: that there seemed to be intelligible geographical patterns in the distributions of interrelated genetic lineages.

BRR. So you needed a word!

JCA. Yes, I needed a word! I coined it in an article for the Annual Review of Ecology and Systematics. And once that was accomplished, I began almost immediately to think in quite different ways about biogeographic topics-- for example, I became more conscious that I was really attempting to use gene trees to decipher the demographic and genealogic histories of conspecific populations-- indeed, that I was thereby actually developing quite a new discipline from the ground up! So, that little lexical exercise offers a fine example of how a well-timed word or phrase can itself profoundly shape one's own thinking. Several other such influential words come to mind. For example, E.O. Wilson coined the word biodiversity about 20 years ago, and it has since become an evocative label for whole areas of biological inquiry. Global warming is another utilitarian phrase that has promoted the recent emergence of several novel research arenas.

BRR. Well, 150 years ago, I don't think anybody was even talking about biogeography per se.

JCA. Exactly, so I suspect there probably was some kind of rather fundamental transformation in the minds of Alfred Russel Wallace and other biogeographic pioneers when the object of their attention first became seen as a formal discipline. "Biogeography" did indeed constitute a beautiful marriage between the formerly separate realms of biology and geography.

BRR. Before we leave this whole idea of serendipity, you call yourself a poster-child for serendipity in your career, but to the extent that might be true, what do you think is the general role of serendipity in the progress of science?

JCA. I think it's often underestimated. I love to read biographies, of scientists especially. When people reflect candidly on their lives, almost without exception serendipitous incidents at key junctures can be seen to have had profound ramifications. Indeed, given that life is inherently sequential, how could it not be the case that idiosyncratic events have huge but unforeseeable impacts on careers?

BRR. And even the people we've been talking about had events in their lives that, if played again differently, perhaps, our science would have evolved in a very different way.

JCA. For sure.

BRR. So, you were already an accomplished evolutionary geneticist before this serendipitous point in your career. Have you thought about, had this not happened, the path your career would have taken?

JCA. Yes, I've often thought about that. If I had never been introduced to mtDNA or become captivated with phylogeography, I'd still like to think that I would have found a useful niche in some other grand scientific arena, such as, perhaps, gene regulation, gamete-based genetics, or con-

ervation genetics. But I certainly have no regrets. I've always been a naturalist at heart, a geneticist in mindset, and an incurable academic who feels forever compelled to marvel at the biological world from novel intellectual vantages. Thus, phylogeography played perfectly into several of my most basic natural dispositions.

BRR. Do you have a message in all of this, then, for today's graduate students?

JCA. Well, just be sure to be lucky as well as diligent! Seriously, if there is any broader message to be taken from my scientific good fortune, perhaps it is to always nurture your deepest interests but also remain prepared to capitalize fully on any unforeseen opportunities that might happen to come your way.

BRR. But you won't know there's an opportunity unless you bring your prior experience to it.

JCA. Quite true! So, here's one more piece of professorial advice: Even as you focus on the daily details of your research, always try to keep at least a part of your brain working in a broadly strategic or synthetic mode as well.

BRR. What's your feeling about the role of a natural history background in this whole business and being able and having the desire to get out and see your system?

JCA. Well, the natural-history side is incredibly important. For example, if I hadn't been raised as an outdoor biologist and natural historian, I wouldn't have had much of any clue about the glorious opportunities that molecular biology provides to study wildlife. To me, one huge problem for the modern world is that fewer and fewer young people have any real opportunity to experience nature firsthand and thereby become enthralled by its wonders. How can we truly care about what we do not emotionally know and love?

BRR. Some people might say that they're even afraid of nature.

JCA. I can attest to that from personal teaching experience. Here I am in the Los Angeles basin, with its 12 million people. Most of my students at UCI have grown up in this impossibly crowded environment and have never, in their entire lives, truly experienced the great outdoors. I find this situation very sad. The good news, however, is that many of these same students do quickly come to appreciate biodiversity after being introduced to even a fraction of its wealth via organismal courses such as ecology or ornithology.

BRR. Yes, and I really wish we could convey that message to certain administrators and developers of curricula these days.

JCA. Yes, for sure. For those students who do have a solid foundation in organismal biology, every other course in a biology curriculum (including such seemingly disparate subjects as genetics, biochemistry, physiology, mathematics, and statistics) almost inevitably becomes far more relevant and meaningful.

BRR. Just in terms of phylogeography being a great integrator between disciplines, I'm wondering what you think its role has been in integrating biogeography back into ecology and evolutionary biology? In other words, what do you think biogeography would look like today without phylogeography?

JCA. I think biogeography would be a poorer discipline in several regards. For example, by focusing on historical in addition to contemporaneous evolutionary processes, phylogeography provides a useful conceptual counterbalance to ecogeography, another major branch of traditional biogeography. Another useful heuristic is that phylogeography fully incorporates and embraces both vicariance and dispersalist perspectives, which traditionally have seemed totally at odds to many biogeographers.

BRR. Have you read, a little bit of a controversial area, over the last decade, a few of the die-hard vicariance or cladistic biogeographers have argued that phylogeography is simply a resurrection of the old dispersalist biogeography that they tried to deconstruct? Do you have any response to that?

JCA. I have a very different take on this topic. I see phylogeography as being an umbrella discipline that encompasses vicariance and dispersalism, both of which clearly can act and interact in particular circumstances to affect the spatial distributions of genealogical lineages.

BRR. I agree with you, and I've argued that it's not resurrecting old dispersalist biogeography because in fact phylogeography's population genetic basis actually makes dispersal analytically tractable.

JCA. And it makes vicariance more tractable too, I might add. Phylogeography doesn't necessarily support one biogeographic worldview against the other.

BRR. Just briefly, if we can look at the broader importance, and ongoing development of phylogeography, we get into this world of theoretical and empirical discordances between gene trees and species trees that we're all very aware of these days, but on the other hand, it seems that mitochondrial or chloroplast DNA trees do frequently capture, as you showed us several decades ago, plausible signals of geographic history that seem to make good biogeographic sense and as such they still seem to nearly always be used as at least a first approximation, even by the most ardent advocates of multiple gene tree approaches. What more do you think we'll learn about biogeography and biodiversity when every-

body's sampling hundreds to thousands of gene trees, and hundreds of co-distributed species?

JCA. Well, that will be a wonderful day if and when it arrives, because everything then should be on more secure empirical and conceptual footings. As you say, much of phylogeography to date has been based on cytoplasmic genomes, merely for reasons of tractability, and yet the vast majority of any species' total genetic history must be ensconced in its nuclear DNA. On the conceptual front, however, most people already have come to appreciate the key distinction between gene trees and species trees, and indeed I take this intellectual conversion to be one of phylogeography's major contributions to evolutionary thought.

BRR. And it's exciting that there are some really bright people working on those issues right now.

JCA. For sure.

BRR. I'd like to finish with you responding to a few broader issues about the impact of phylogeography. The first I was thinking of was the impact of phylogeography in making progress toward developing a unified and operational species concept.

JCA. I think we already have gained a much richer understanding of "species" than we had before the phylogeographic era, and a lot of this improvement goes back to the basic gene tree – species tree distinction. Personally, I've always been quite content with the basic sentiments of the BSC (biological species concept), but I'm also cognizant that we can probably learn some things from the PSC (phylogenetic species concept) as well. Actually, I think that the BSC and PSC can and will ultimately be reconciled, at which time the whole debate may be remembered as little more than a semantic brouhaha. If such a reconciliation does indeed eventuate, I think we can then thank phy-

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logeography (and the clarity of its basic distinction between gene trees and species trees) for having contributed substantially to a final resolution of "the species problem".

BRR. Related to species concepts and biodiversity, what do you think of phylogeography spinning off concepts such as ESUs and initiatives such as DNA barcoding? Are these worthwhile and valuable endeavors?

JCA. I'm quite happy with such developments. The ESU concept is important because it emphasizes that there can be rather deep historical subdivisions within species that may warrant special conservation and taxonomic attention. The related but different concept of the MU (management unit) is important too, because it brings contemporary demography into the picture as well. Taken together, such concepts have stimulated deeper thought about what population structure means at different temporal levels and spatial scales, and from different evolutionary etiologies. With respect to DNA barcoding, I have more mixed feelings. On the one hand, I've long been an advocate for greater standardization in biology, especially in the field of systematics, and DNA barcoding is one practicable route to such an end. On the other hand, a potential downside is that people might become unduly enamored with single-gene data that sometimes may misrepresent broader genetic relationships.

BRR. Related to those concepts is the overall contribution to conservation of biodiversity. Do we know more about biodiversity and how to conserve it because of phylogeography?

JCA. Yes, definitely. For example, we can now appreciate more fully how biodiversity relates to phylogeny, and that these terms can apply at multiple levels, ranging from the gene at one end of the biotic continuum, to species, and to regional biotas and ecosystems at the other end. Most fundamentally, biodiversity is simply the richness of life, which ultimately is the richness of the planet's genetic heritage. So, I think phylogeogra-

phy has been extremely helpful in revealing that richness. More specifically, I like the whole idea of implementing a nature reserve system focused on biodiversity, much as our current national parks seek to preserve rich geological features such as Yosemite's scenery or Yellowstone's geysers. Wouldn't it be wonderful if society could get its act together well enough to put together a series of parks that feature biodiversity as well?

BRR. It would be fantastic. Even concepts such as wilderness areas tend to be areas that are not very useable for other things that other people wanted to use them for.

JCA. Yes. If the nation were to establish a series of what we might call biodiversity parks, an important component to understanding where those parks should be placed is not only extant biodiversity but also historical considerations— where did this modern biodiversity come from? Much as national monuments recognize important events in human history, key happenings in the Earth's natural history could be captured by appropriately placed biodiversity parks. Such phylogeographic reserves might even spark a new societal conservation ethic, when enough people finally learn to enjoy, appreciate, and cherish the Earth's biological heritage.

BRR. So are you thinking something along the lines of phylogeographic hotspots?

JCA. Yes, that could certainly be a part of the biological rationale underlying choices about where to place the parks. You would want to take into consideration not only what's currently there but also how what's now there came to be.

BRR. So the whole biodiversity parks concept is very integrative and synthetic in its own right?

JCA. Yes.

BRR. That feeds into my last question, which is the contribution to scientific literacy as a whole, and I think that you've kind of come up with a boots-on

-the-ground idea about converting what we all think about into broadly something that people can see and increase their scientific literacy. Do you have any other thoughts on this?

JCA. Imagine people visiting one of these biodiversity parks. I would assume that they might go first to the visitor's center where they would be exposed to films and exhibits on how the geographical and biological histories of the region mesh. And then as they further explore the park, the entire learning experience would be highly enriching. People might then want to tour more such biodiversity parks, to get a fuller sense of history of a continent (or even of the world when an entire network of parks becomes internationally linked). I can see endless educational opportunities, and the more the public learns about biodiversity, the more enthused it is likely to become about protecting the planet's biological heritage for future generations. Especially in democratic societies, widespread public awareness about biodiversity can only help to move governments toward wiser conservation policies.

BRR. And the fact that our appreciation for biodiversity is not conflicting with an appreciation for human well-being?

JCA. The two are in fact essentially one-and-the-same.

BIOSKETCH: John C. Avise

Even as a youngster I was an enthusiastic naturalist, determined someday to translate that fascination into a profession. Toward that end, in 1970 I earned a B.S. in Fishery Biology at the University of Michigan in Ann Arbor. Two more degrees followed: a M.A. in Zoology from the University of Texas at Austin in 1971, and a Ph.D. in Genetics from the University of California at Davis in 1975. I spent the next three decades at the University of Georgia in Athens, where I worked my way up the academic ranks before moving in 2005 to my current faculty position at the University of California at Irvine.

Temporally, my career paralleled the rise of molecular biology in the latter half of the 20th century, and I have consistently tried to capitalize upon that good fortune by applying molecular markers to intriguing questions in natural history and evolution. Thus, I am a molecular ecologist and evolutionary geneticist with an abiding love of nature and an endless intellectual compulsion to unravel its many mysteries. My rather atypical career in the natural sciences is detailed in an autobiography published in 2000: *Captivating Life, A Naturalist in the Age of Genetics*.

In addition to conducting research in such areas as phylogeography, conservation genetics, and molecular natural history, I have tried to communicate the wonders of science to a broad audience by publishing more than 20 textbooks and tradebooks on various evolutionary, ecological, and genetic topics. I have been blessed throughout my career not only with fabulous students and colleagues but also with a wonderfully supportive wife and daughter. Ultimately, these people deserve much of the credit for any lasting scientific contributions I hope to have made.



Picture from <http://today.uci.edu/>.