ES: We have one final large presentation, longer presentation, this afternoon by Dr. John Avise, from the University of Georgia, who ll be talking to us on The History and Purview of Conservation Genetics. Essentially summing up the entire field in 25 minutes. I wish him luck.

(Applause)

THE HISTORY AND PURVIEW OF CONSERVATION GENETICS

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JA: Well, I d like to join the other speakers in thanking the organizers of this conference. It s really a pleasure for me to be here and to hear this discussion on conservation biology; to see lots of old friends, and to, perhaps, make some new ones.

Now, the task that I was given for this afternoon is a rather daunting one. It has been to try to characterize the history of this field that we call conservation genetics. And so I m going to bite my lip very tightly and try to not give any data from my own lab, or go into our own personal experience with this field but, rather, to take that charge seriously and see if I can give you some sense of, at least, my perception of what conservation genetics has been and is becoming. It s clearly an evolving discipline.

Now, certainly, most biologists and, hopefully, many others are increasingly recognizing that the direct and indirect effects of human population growth are currently precipitating dramatic losses of biodiversity around the world. And at these meetings we ve certainly heard some very eloquent presentations that just touch on the scope of that problem. It s incredible. In their recent textbook, Gary Mefee and Ron Carroll have defined the field of conservation biology as, quote, a response by the scientific community to this biodiversity crisis. End of quote.

Now, ultimately, I think that biodiversity is genetic diversity that is, a product of the evolutionary process. If you follow that reasoning, then it would be quite logical to suggest that conservation genetics might be defined as, quote, a response by the scientific community to the genetic-diversity crisis. However, any description that s that encompassing I think is needlessly vague. And, furthermore, it doesn t really greatly illuminate what most self-described conservation geneticists actually do for a living.

At the other end of the scale, conservation genetics has often been narrowly characterized in the literature as a discipline devoted primarily to the study of inbreeding effects and the loss of adaptive genetic variation in small populations. And I think that definition is unduly restrictive, as evidenced by the fact, as I ll show later, that it ignores the primary research agenda of more than 60% of all published scientific articles that were designated by the authors, themselves, as belonging within this field of conservation genetics.

Now, with the proliferation of molecular technologies beginning more than 30 years ago, the scope of conservation genetics unquestionably expanded greatly. Genetic diversity, as we ve heard, is now analyzed directly and routinely at many levels, ranging from heterozygosity issues within individuals and local demes to patterns of geographic variation in gene flow, to species differences and issues regarding hybridization and introgression, to phylogenetic patterns at any depths in the tree of life.

Conservation-genetic research is often targeted at imperiled species but, I would argue, it can also be geared toward regional or landscape issues. The whole field of phylogeography is very much concerned with that, for example. Or towards gaining conservation lessons from studying populations, species or taxonomic assemblages that are not imminently threatened with extinction. Indeed, I think that s where many of our most important contributions in the field will come from is simply learning about nature; about life; about how it works. And that can be done studying genetic processes in all sorts of organisms, including those that aren t immediately threatened with extinction.

So here I want to take sort of a middle ground by defining, if you will, conservation genetics as the study of ecological-genetic, or evolutionary-genetic or even molecular-genetic patterns and processes within an explicit framework of preserving biodiversity, and the natural forces that foster that biodiversity.

Now, adopting that orientation, I d sort of like to begin the talk today by providing a brief chronology of some landmark historical events in the ongoing maturation of conservation genetics, as a recognizable component of the broader field of conservation biology. And I want to present this thumbnail sketch I kind of feel embarrassed, almost, to do so. I d like to do it with all due apologies to many researchers, who I can t mention here for lack of time, but who have also made many highly significant contributions to the field.

So I m just going to touch on a few of what I think of as sort of eclectic examples of landmark events in the recent history of conservation genetics. The events that I ll mention range from singular breakthrough discoveries to the initiation of extended case histories of special historical importance to the field; to the publication of some seminal contributions or synthetic works; to events of even special political or social significance.

And I guess, if anything, the take-home message from this little thumbnail sketch which is elaborated, I might say, in the written paper that accompanies this talk /that ll, hopefully, appear in the proceedings of this meeting I guess I hope that the take-home message might just be to remind some of you how temporally shallow or recent the whole discipline of conservation genetics is.

So let s just go back to, if we can start, about in 1966. Dick Lewington and his colleagues I m just going to give some of these events here introduced molecular methods namely, protein electrophoresis to population biology. That s less than 40 or so years ago. Many students today often seem to think that molecular genetics and population biology have always been intimately related and closely allied disciplines.

That s far from the truth. When I began graduate school myself, there was virtually no communication whatsoever between those disciplines. And this meeting today is testimonial to how that state of affairs has changed dramatically. We now take quite for granted that molecular biology and molecular genetics can inform us tremendously about the natural biological world and, in some cases, have immediate conservation relevance.

An important political event, if you will, was the Endangered Species Act of 1973 in the United States. This set a legal precedent and incentive in this country to identify and conserve rare taxa. Now, the importance and effectiveness of this landmark legislation have been rightly applauded for example, by this 1995 book-length report from The National Research Council. That basically pointed out the effectiveness of this legislation, despite its many evident flaws.

In 1979 I m just going chronologically through some things Elizabeth Ralls and her colleagues drew attention to the widespread occurrence of inbreeding depression in captive populations a fairly novel concept at that time. Also in 1979 my colleagues and I and, independently, Wes Brown and his collaborators introduced mitochondrial DNA approaches to population biology. It never occurred to me at that time that I might seek patents for that kind of an approach, nor did I talk to any lawyers. (Laughter) I wish I d thought about it. (Laughter) I guess things have certainly changed for the better, haven t they? Here we are today, surrounded by lawyers, as well.

In 1980 Michael Soul and Bruce Wilcox published the first of several conservation genetics books, that took an explicit evolutionary-genetic as well as an ecological orientation. In 1983 Christine Shonewald Cox and her colleagues edited the first major volume devoted explicitly to genetic perspectives in conservation.

I think, in many respects, if we had to put sort of a formal birthdate on the field of conservation genetics, it might be 1983, with the publication of this rather seminal work. Also in that year Steve O Brien and his colleagues initiated an important series of studies on inbreeding, genetic heterozygosity and population bottlenecks in wild felids work that continues to this day, and is surely one of the classic examples extended examples in the history of conservation genetics.

In quite a different area, *Carrie Mullas in that year, 1983, invented the preliminary chain reaction for *in vitro* amplification of DNA from even the tiniest bits of tissue. One year later, in 1984, Alan Templeton and his colleagues initiated a series of influential studies on captive breeding programs, aimed at avoiding inbreeding depression in bovid species.

In 1985 The Society for Conservation Biology was formed. And Alec Jeffries and his colleagues in England introduced DNA fingerprinting methods to population biology, and advocated their forensic utility particularly in studies of parentage and in pedigree analyses. In 1986 Ollie Ryder stirred the waters by bringing the term evolutionarily significant unit, or ESU, to wide attention in conservation biology. A theme that s later been followed by Craig Moritz and many other researchers.

In 1987 Nils Ryman and Fred Utter edited a volume on population genetics in fisheries management. And, also in that year, the first issue of *Conservation Biology*, the journal, was published. And that complemented earlier journals in the field, such as *Biological Conservation* and *The Journal of Wildlife Management*. Also in 1987 my colleagues and I introduced the term phylogeography, and outlined that field s major principles a discipline that s concerned with the historical component of population structure, and how genealogies are distributed across a landscape. Even for multiple codistributed species, in some cases.

In 1988, in a *Science* article, Russ Landy focused attention on genetic versus demographic concerns for small populations and that s been a very stimulating article for, I think, subsequent thought on the connections, rather than the distinctions, between genetics and demography in conservation efforts. They often, jointly, are in mutually informative kinds of approaches.

Several important events took place in 1989. The Captive Breeding Specialist Group began a series of studies on population viability analyses for endangered taxa. Out in Ashford, Oregon, The U.S. Fish and Wildlife Service opened a laboratory facility devoted explicitly to wildlife forensics an important component of which was genetic analysis. Microsatellites were introduced by a number of researchers as a source of polymorphic nuclear gene markers in that year.

Also just to get a little personal advertisement in for one of my former students Brian Bowen in my lab published the first in a long series of papers on the global phylogeography and phylogenetic issues in marine turtles all seven species of which are endangered or threatened. And that, among other things, brought I think, to a broader audience the multifaceted applications of genetic research to endangered taxa in the wild.

In 1991 Richard Bainwright and his colleagues raised several novel issues about phylogenetic diversity and the whole topic of conservation worth something that is still very much debated to this day.

Another of our speakers, Kent Holsinger together wit h Don Falk in 1991 edited an important volume on conservation genetics in rare plants. A year later, in 1993, Nancy Thornhill edited an important volume on the natural history and consequences of inbreeding and outbreeding. Again, I m just touching on a few things and I hope people will forgive me that have a different impression of what was important. But these are just some events to give you some sense of the time scale of our discipline.

In 1994 it seems like another life, to me, ago, but it was just a few years ago I published the first major textbook that attempted to summarize the many applications of molecular-genetic approaches to ecological and evolutionary questions. And, also, those of conservation biology which constituted the final or concluding chapter of that work.

Also in 1994, Terry Burke edited the special issue of *Molecular Ecology* that was devoted explicitly to conservation genetics. And in that year and there are studies of several cetacean species, as we ve heard from Steve Palumbi he and Scott Baker and their colleagues provided the first of a stunningly powerful series of applications of molecular forensics. In this case in monitoring the products from endangered cetacean species in commercial markets.

In 1995 Jon Ballou and his colleagues edited a volume on genetic and demographic management issues for small populations. And a year later, in 1996, *two* edited volumes appear, that provided the first compendia of molecular studies in conservation genetics. One was edited by myself and Jim Hamrick, and the other by Tom Smith and Robert Wayne. Most of the case histories that were summarized in these two volumes addressed genetic issues in natural, as opposed to captive, populations.

In 1998 Fred Allendorf edited a special issue of *The Journal of Heredity*, devoted to conservation genetics of organisms in the marine realm again, highlighting how genetic studies need not be confined to small or captive populations. They can be used to address a whole host of issues that basically just tell us about how organisms behave; their natural histories; their ecologies much of which is relevant to conservation efforts.

In 1999 Laura Landweber and Andy Dobson edited a volume on genetic issues in species extinctions, and in an important article in *Biodiversity in Conservation,* Wilt and Wemmer reviewed and previewed various reproductive technologies, such as artificial insemination, cloning, embryo transfer, and the like in conservation efforts.

Last year, in the year 2000, I published the first textbook on phylogeography. As I ve mentioned, a field that has a very strong genealogical slant on genetic variation, even within species and, I would argue, has considerable relevance to conservation efforts, as outlined in that book. Also, last year a new journal was launched, *Conservation Genetics.* And finally, here we are in 2001, where an important symposium entitled Conservation Genetics in the Age of Genomics was held, I heard, somewhere in New York. Well, conservation genetics is inherently sort of an applied science, and yet it s so tightly allied to the basic life sciences as to grade continuously into the latter. These time-honored disciplines include ecology, and natural history, ethology, demography, population genetics, evolutionary genetics, taxonomy, systematics and phylogenetics.

Thus, to cleanly demarcate the purview of conservation genetics is a difficult task, at the least and, at least, an arbitrary task. The job is further complicated by the fact that research orientations in conservation genetics have shifted somewhat through time. Concerns about inbreeding depression have always been a major theme. But, in recent years, molecular-genetic assays, as well as novel reproductive technologies, have opened a far wider world of research opportunities within the field.

So this slide I guess you can t, probably, read this very well. But there s a number of different foundational roots of conservation genetics that are tied to the basic biodiversity sciences, and these include the whole field genetics and genetic theory which encompasses population genetics, evolutionary genetics. Then there s this whole discipline of molecular genetics, which has been very much a focus of these meetings here. And then the traditional biodiversity sciences ecology, natural history, ethology, systematics and the like.

Now, these fields, of course, communicate, increasingly, with one another, and they all feed into this big component here that I call application-for-conservation issues. And it turns out that there s a number of different subdisciplines within this field that I call conservation genetics that range from within population issues, through forensics and monitoring, on into manipulative sorts of topics. And I ll come back to this slide later and elaborate on it at greater length.

Okay. So to appraise what practicing scientists, at least, mean when they employ the words genetics and conservation jointly, in preparation for these meetings I conducted several computer-based searches of the literature, using the key words genetics and conservation, or conservation genetics. And in those computer searches I identified more than 600 papers that came up using these search terms. Now, clearly, these include only a tiny fraction of scientific papers actually germane to the field of conservation genetics but, nonetheless, perhaps they provide at least a crude guide to the emerging scope of the discipline.

After a lag period in the 1980s, if we start back here, with Shonewald and Cox s publication, *Genetics and Conservation,* and go forward in time, the number of published articles in the field of conservation genetics has approximately doubled in each successive two-year interval during the 1990s. Now, this explosive growth of conservation genetics has generally paralleled the expansion of conservation biology writ large which, itself, has reflected, of course, a heightened awareness by the scientific community of a global biodiversity under tremendous siege.

Now, in scanning through those 700 or so papers, approximately two-thirds of them involved empirical molecular-genetic approaches. Another one-sixth or so involve nonmolecular empirical approaches to conservation genetics, and about a sixth of the papers I would categorize in the area of population-genetic, or evolutionary-genetic, theory, as applied to conservation issues.

Now, based on those literature searches this is that slide you ve seen earlier, many times? the current purview of the field, I think, can sort of be divided into at least six overlapping subject areas, as identified at the top of this slide. And, again, you probably can t read all of these, but we ll go through them in greater detail in a minute. And this is, of course, an arbitrary division on my part. One could slice the pie differently and come up with different sort of categorizations. But I hope you ll find this useful as a heuristic exercise.

So there are, within population issues, geographic-variation issues; species-diversity issues; forensic applications; monitoring applications; and manipulative sorts of applications. What I want to do is go through each of those in turn ... and those are sort of labelled with these letters A through F. And this, on the top, is sort of a percentage of those 700 articles that dealt with those various topics.

First, within population assessments, about 30% of the journal articles that I identified in my computer searches had focused primarily or exclusively on genetic issues within single small populations either domesticated, captive or wild. Inbreeding, and associated losses of genetic variability and fitness, were the most common recurring themes, but some of the papers also addressed related issues, such as the long-term demographic history of a population, as deduced from genetic data, or behavioral-genetic findings, such as kin recognition or microspatial dispersal in the context of reproductive modes in mating systems.

Now, deleterious effects of inbreeding have been known for centuries and were highlighted in domesticated plants and animals by Charles Darwin. Post-Mendelian genetic studies of inbreeding began early in this century, and the genetic causes and ramifications of inbreeding depression remain important issues today. Thus, I found it of little surprise that the avoidance of inbreeding depression was a major theme in this literature search in these papers, together with demographic considerations, and that it s become an important issue in the design of modern captive-breeding programs and in assessing the, quote, genetic health of small inbred populations in nature, as well.

A lot of the early studies examined inbreeding effects on fitness components, such as viability or fertility. But, following the introduction of molecular-genetic approaches, the consequences of inbreeding could also be assessed in terms of lowered heterozygosities at specifiable loci. And this soon lead, historically speaking, to the widespread use of molecular data to estimate genomewide variability from various kinds of markers. And then those estimates, in turn, were often viewed as surrogate measures of a population s genetic health or adaptive potential. And endless debate has gone on about how valid those kind of extrapolations might or might not be in particular instances.

Geographic-variation issues second category. Given the long history of interest in inbreeding and its relationship to genetic fitness, I was sort of surprised, in the literature search, to discover that even more conservation-genetic articles self-described articles, as being in the conservation-genetics realm had focused on multipopulation issues. About 45% of the articles fell into that category. These, typically, addressed questions of population structure, dispersal, gene flow, or the delimitation of genetic or demographic stocks within a species all in the context of conservation or population-management issues for particular species.

Now, there are two major subareas within this category that were evident phylogeographic topics and what I ll call population-structure topics. The population-structure analyses typically analyzed spatial variation and allele frequencies at allozyme loci, or microsatellite loci, or other nuclear genes. Phylogeographic studies, by contrast, typically analyzed mitochondrial gene trees or, less often, other sorts of gene trees. Now, traditional population genetics and phylogeography both deal with spatial genetic patterns, although they have rather different conceptual orientations, quite often, in their treatments of that spatial structure.

Species diversity issues. Under this broad category I ve included studies that dealt with speciation, hybridization and phylogeny that is, with genetic issues at and above the level of taxonomic species. At least as they re recognized, traditionally, in the literature. About 15% of the papers in my computer search involve such topics. And, yet, given the vast, broader literature on speciation, introgression and molecular phylogenetics, these clearly represent only the tip of a vast iceberg of papers that would have at least tangential relevance to conservation efforts.

Another fairly distinct category of papers was in this area of forensics. About 5% of the papers in my literature search proved to focus on wildlife forensics by which I mean the genetic identification of plant or animal products of otherwise uncertain origin.

Now, there s at least two biological settings where that kind of information has come into play and been relevant. First, it was often of scientific interest to analyze the genotypes of shed products such as hair, or feathers, or skin or feces thereby obviating the need to capture, or otherwise disturb, free-ranging animals that might be of conservation concern. And, second, because of the extensive illegal trade involving many protected species, it is often necessary for law-enforcement agencies to determine the biological source of confiscated wildlife products.

Now, a great boon to such noninvasive forensics was, of course, the invention of the preliminary chain reaction, or the PCR a technique that, for the first time, permitted the *in vitro* amplification of particular stretches of DNA from even the tiniest bits of starting tissue.

Another topic identified in this search of the literature was environmental monitoring. A handful of distinctive papers that I found in the computer search dealt with genetic markers as tools for monitoring the biological impacts of chemical toxins, pollutants, or other kinds of environmental insults. Such studies typically addressed either the mutagenic effects, per se, of exogenous chemicals, or other population-genetic consequences of environmental stresses and disturbances.

Finally, genetic and reproductive manipulation. Everything I ve described so far is pretty much descriptive. But, then, there s this whole topic, nowadays, that we ve heard a lot about at these meetings, of active genetic manipulation rather than mere description of the natural world. Although my targeted computer search failed to identify any journal articles in this area of direct genetic manipulation in a conservation context, I nonetheless include this category because it may well become an identifiable subject area in the field of conservation genetics in the fairly near future.

For example, I think it is quite likely that *in vitro* fertilization, artificial insemination, embryo transfer, organismal cloning, and many other manipulative reproductive-genetic technologies will soon become fairly standard practice, for better or for worse, in the active management of threatened species.

Now, of course, reproductive and genetic efforts often grade into one another. For example, more than 15 years of research into the refractory reproductive biology of the cheetah has finally yielded successful techniques for the artificial insemination of that species using fresh, as well as frozen, sperm. And these methods, in turn, can and are being used in breeding programs to minimize inbreeding in that large cat.

A related research area that Ollie touched on a bit is in the *in vitro* maintenance of gene resources in organized banks of DNA, or germ plasms, or tissues. Cryopreservation of gametes and other cells is one such example.

And, finally, I think an important emerging area or an area that s likely to become increasingly important in what might be called conservation genetics will be in assessing the potential ecological genetic benefits, as well as risks, of genetic engineering, and the release of genetically modified organisms into the environment. That, soon, too, may fall within the recognizable sphere of what we call conservation genetics.

Well, in conclusion, my attempt has been to define and characterize the purview of conservation genetics, in order to help expand, rather than circumscribe, this evolving subdiscipline of conservation biology. If you want to define [it] some way else, that s fine. I m really not trying to be restrictive in my definitions, but, rather, expansive, in what I think we might view as logically falling within this realm.

At the same time I can t emphasize this too mu ch I don t want to be interpreted as claiming undue priority for genetic concerns within the broader field of conservation efforts. Although genetic methods and perspectives can be empirically and conceptually illuminating and, certainly, intellectually stimulating and they can often assist in conservation efforts, they re merely one very small, yet integral, part of a much, much larger mission.

The truly pressing issue, of course, is whether biodiversity and the ecological and evolutionary processes fostering its maintenance can be preserved more or less intact during what will be a very pivotal 21st century in the history of life. The current biodiversity crisis, as many people have correctly pointed out, is, of course, fundamentally, a problem of environmental alteration and habitat loss under the collective weight of burgeoning human numbers. No genetic efforts, however valiant, can make more than a tiny dent in solving the greater problem, which will require the full engagement by all of the life sciences, as well as enlightened societal attitudes and strengthened political will.

I hope that we, as a global society, will not act like this endangered species, the pocket gopher, is, and bury our heads in the sand. Rather, I hope we ll try to rise to the task before us. But it s a huge one, and we re going to have to avoid getting depressed all the time in trying to deal with it.

In any event, that s with respect to this talk, that is the end. So thank you.

(Applause)