
Photo: John and Karen Hollingsworth

A conversation with Russell Lande, London

"Who's Going to Speak up for Nature?"

Theoretical biology may not be the most fashionable topic. Nevertheless, the Italian-Swiss Balzan foundation offers one of its prizes for exactly that field. A field that has ultimately also helped this year's awardee, Russell Lande, in court to save the Northern Spotted Owl, threatened with extinction by the activities of logging companies.

Lab Times: There is a great photograph of you on the internet that shows you as a 19th century explorer. Do you feel like one?

Lande: I definitely feel like an intellectual explorer, yes. An exciting thing for me is the history of intellectual exploration in all kinds of fields. One of my hobbies used to be reading biographies of famous scientists. It's difficult to tell if something is worth exploring or inventing. Maybe a combination of those. I actually also spent a year of my life in remote tropical jungles of Central and South America, which certainly recreated the experience of explorers, too.

This is quite a contrast to the methods you use, such as mathematics and statistics, that are difficult to grasp for biologists like me. Why are they necessary for your research?

Lande: Evolution and population ecology rely more on theory than any other area of biology. These are very conceptual topics. The concepts help people thinking about it. It's also a sign of any mature and developed science, when it becomes very quantitative.

Are these methods a way of dealing with randomness, which is maybe not so important in other fields of biology?

Lande: Yes. In most cases I would call randomness a quantification of ignorance. Randomness means it's unpredictable. I think the only really true randomness is at the quantum level. Most sciences have to deal with a combination of deterministic and stochastic processes. When it comes to evolution and change of population size these random factors are pretty accurate descriptions of probabilities of what would be happening.

You are credited for taking quantitative genetics from the breeding of animals and plants to natural populations. What did you have to change?

Lande: The main thing is that the theory of inheritance of multiple characters was very well developed but the theory of selection on multiple characters was almost non-existent. Natural selection indeed acts simultaneously on multiple characters. This has been understood since Darwin.

> "In most cases I would call randomness a quantification of ignorance."

That's different in breeding?

Lande: Yes. In animal breeding, even if they are interested in improving multiple characters like the number of eggs, as well as the size and the quality of eggs. They make a selection index. Let's say that weight per egg is twice as economically important than the number of eggs. They make a linear combination of the characters that they treat as one character and then select the best index. That gives them the most rapid economical improvement, which is the best thing to do in breeding but is generally not how natural selection works. Natural selection is not always acting in a directional way. It's acting towards a joint optimum...

Russell Lande

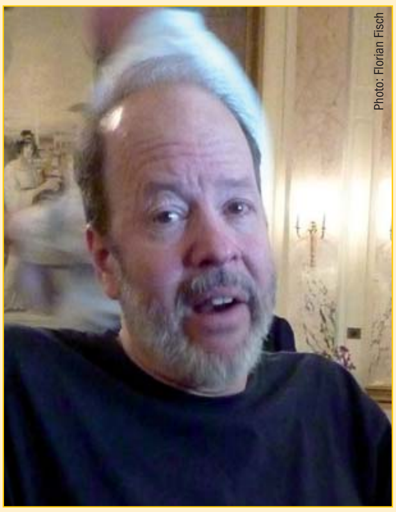
Photo: Florian Fisch

...received his PhD in 1976 from Harvard University. The US-American evolutionary biologist and population ecologist, single author on many papers, was recently awarded the Italian-Swiss Balzan prize of "theoretical biology" "for pioneering contributions to the development and application of theoretical population biology, including the modern development of the theory of quantitative genetics, and the study of stochastic population dynamics". In other words: Lande applied mathematics and statistics to evolution and ecology.

Lande developed models for the selection of correlated traits. He brought the theory of quantitative genetics from breeding to wild populations. However, Lande is not just a theoretician. The biologist contributed to establishing the red list of the International Union for the Conservation of Nature (IUCN). Lande sees himself as a researcher rather than a teacher. Something he has been able to do since 2007 in his position as a Royal Society Research Professor at the Imperial College London.

...so you added complexity to the theory?

Lande: Yes, I developed the first theories about natural selection acting on multiple quantitative characters. For example, how to identify, which set of characters selection was acting on.

So, before that, people studying natural selection were purely focused on discrete characters?

Lande: They were also studying continuous quantitative characters. But when it came to natural selection, even Haldane, one of the founders of the modern synthetic theory of evolution, was only analysing natural selection on a single character. But you don't even know that the selection that you see is caused by selection on that character – phenotypically or genetically. That's the age-old question. Even before selection was understood, people knew that characters were not independent. People that have big arms usually have generally big bodies. Many characters are correlated with each other and with overall size. Eventually, the inheritance was understood but the understanding of selection was decades behind.

What's the difference between selection and inheritance?

Lande: The inheritance just tells you about the transmission genetics that causes a phenotypic resemblance between related individuals. But that doesn't have anything to do with natural selection. It doesn't tell you anything about the direction of natural selection or the combination of characters that selection favours. Once inheritance was resolved, evolutionary biology almost forgot about it. The geneticists started studying genes more and more, which is understandable. The basic microscopic mechanism is clearly of fundamental importance but you can't understand high level processes solely by understanding mechanisms at the low level. Obviously there are many intermediate levels where people have to make descriptions that work with a certain degree of accuracy, so they can actually understand instead of simulating every subatomic particle.

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Did these correlated traits also bring you to study sexual dimorphism?

Lande: Yes, they are also correlated. For example, if you take *Drosophila* and you select males for larger body size what you see is that both male and female size increase almost in parallel. So, genes affecting body size have almost the same expression in males and females. If you select males and females in opposite directions, you get a much slower response. This is because there are relatively few genes and a small amount of genetic variation to account for the difference between the sexes.

How do extreme dimorphisms like the peacock's tail evolve?

Lande: That involves another thing: female mating preferences as a character acting on the really extreme male characters as in the peacock or in stalk-eyed flies. In some fly species the distance between the eyes is longer than their body. The Darwin-Fisher scenario, which I was the first to model, deals with the male character as a morphological character and the female character as a perceptional character as basis for the choice of mates. They are controlled by completely different genes. If both characters are genetically variable, then females that have a genetic preference for mates with long tails produce sons with both the genes for long tails and the genes for stronger female preference for longer tails, which the males don't express.

Assortative mating as well as selection can cause a genetic correlation of characters that are determined by completely different sets of genes. This creates a positive feedback loop in Fisher's runaway sexual selection process. Fisher obviously knew this but he used a shorthand verbal description, so that biologists can understand it more easily. Fisher's verbal description misled most people into thinking that female mating preferences were always adaptive. But in his original scenario with no direct cost to choosiness, they are actually selectively neutral. Now, people are trying to understand if there may be some cost to the preference, which is something else.

Photo: Florian Fisch

Why did you get interested in these topics as a student?

Lande: My initial interest as an undergraduate was applied ecology and the effects of humans on the stability of ecological systems. In the early 1970s, ecology was a popular subject and it still is today. I was very interested in theoretical ecology. Unlike theoreticians who start from a maths background. I could see that the theories of community ecology were too simplistic, that they were going to eventually collapse and that's what happened. So, I started studying evolution initially to gain a deeper understanding of how ecological communities were organised.

"There is still a huge uncertainty about how ecosystems work, making it easy for lawyers and politicians to promote or allow their degradation and destruction."

I soon discovered important areas of evolution that had been neglected for a long time and so I got absorbed by studying evolution for its own sake. After 10 to 15 years, I felt that I'd done most of the important things I could do in evolution and I got involved in conservation and basic ecology. I saw that, especially in the early days of conservation biology, theories applied to breeding small populations and endangered species in zoos were starting to be applied, without thinking critically, to wild populations in changing environments. So, I started working in those areas to correct a lot of misconceptions.

Did you introduce randomness into population dynamics used for conservation biology?

Lande: I wasn't the first one. But I developed the theory and elucidated a lot of new types of interactions caused by stochasticity.

"It turned out to be the biggest environmental court battle of the decade."

Your stochastic theory is used by the International Union for the Conservation of Nature (IUCN)...

Lande:...Well, it's used in a very general way. I helped the lead person, Georgina Mace, in designing the initial version that was adopted, with some modification, to classify the extinction risk of species in all countries around the world. The IUCN explicitly shies away from using stochastic models because it's difficult, especially for endangered species, to get enough ecological information to estimate the stochastic parameters. Deterministic processes are usually the processes that cause species to become endangered to begin with, unless they are naturally rare. Stochastic processes usually become important for extinction risk only after the species have been driven to low levels. They are not usually the cause for endangerment but the final process, the symptom.

*You're said to have saved the Northern Spotted Owl (*Strix occidentalis caurina*) in the American northwest. You used an inverted model for pest control in farming to calculate the required territory for the Owl's survival. How did this work?*

Lande: The model was developed by Richard Levins for control of pest insects in agriculture and refined by Ilkka Hanski for use in conservation. The main applications of these ideas were finally introduced into conservation biology, actually metapopulation biology. All those theories are most accurate for species that are not territorial. Many bird species hold individual territories. The habitat that the owls require is 150 to 200 years old growth forest.

Commercial forestry has fragmented their habitat since World War II. I developed a simple model where the territories held by an individual couple were either suitable or not suitable. So I was able to connect together the individual age-structured demography with the metapopulation theories. The question I was trying to answer was: what is the minimum amount of habitat of suitable patches randomly distributed across a landscape? I was also able to connect the dispersal behaviour of juveniles searching for a suitable unoccupied territory. Whether they can find such a territory or not before they die from starvation or predation. I came up with some pretty simple general results, even though it involves a lot of parameters.

By law, the US government is supposed to protect the habitat of all native vertebrate species on government-owned land. The US Forest Service was basing its original conservation plans on the minimal population size in order to maintain enough genetic variability to adapt to a changing environment. It was ultimately based on the mutability of quantitative characters that I had analysed in my PhD. In other words, it was based on no ecology whatsoever, except the idea that these patches of suitable habitat should not be farther apart than the farthest distance ever observed for dispersing juveniles. So, you can see how simplistic this was. They had no idea at all, whether these patches would be occupied or not. I was asked to look at this.

You testified in court, didn't you?

Lande: My analysis of the data on spotted owls, which led to nearly a thousand pages of court transcripts of my verbal testimony, showed that the US government plans were likely to drive the Northern Spotted Owl to extinction. It turned out to be the biggest environmental court battle of the decade. I was the key expert witness in the law-suits against three branches of the US government responsible for management of wildlife that were brought up by conservationists.

How was it for you to be in court as a scientist?

Lande: No matter how many shows about lawyers you watch on television, you don't fully get the impression of how ignorant and how hostile the questioning is that an expert witness receives.

Did you feel like the accused?

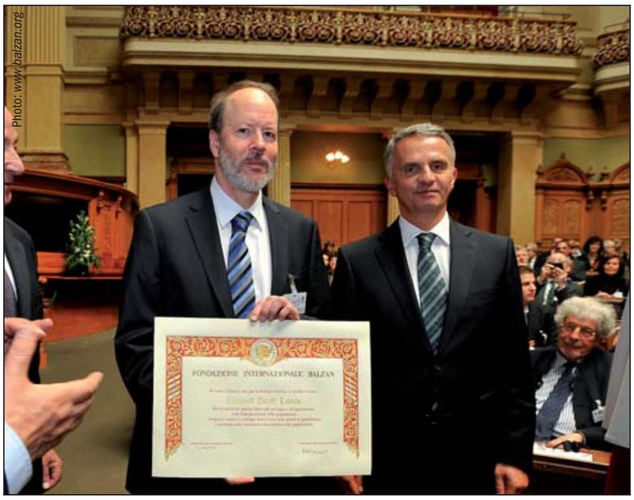
Lande: I felt that I was on trial and most of the effort by the government lawyers as well as the timber industry lawyers was to discredit me as a witness, rather than getting at the substance of what I had done. I didn't ever get any money out of this, which of course meant that the timber industry lawyers tried to make out that I was some sort of a fanatic and biased. But they would have made the same arguments if I had gotten paid. Lawyers can twist an argument almost any way.

They didn't understand...

Lande:...Mostly they didn't. The timber industry lawyer was the only one who was high paid and the timber industry was the only one who could hire enough expertise to ask me critical questions about the substance of what I had done. And that's typical of how scientific experts are dealt with in law courts.

"If you are too highly trained, you're stuck in traditional ways of thinking and it's difficult to break out."

You wrote in your book that "extinction is the eventual fate of all species". Why should we really care about the Northern Spotted Owl?



Russell Lande (left) receives the Balzan Prize 2011 for theoretical biology from the then Swiss interior minister Didier Burkhalter (right).

Lande: Currently, the rate of species extinctions due to human actions on land and in aquatic environments is roughly a thousand times the natural rate of species extinctions. The Northern Spotted Owl, like African elephants, is important because it is one of the species with the largest habitat range requirements – it needs old, undisturbed forest. It was viewed as what is called an umbrella species. Protecting the habitat of that species and the species itself would protect an entire ecosystem that was in danger of being eradicated because of commercial logging.

"Currently, the rate of species extinctions due to human actions on land and in aquatic environments is roughly a thousand times the natural rate of species extinctions."

And that should be protected for beauty?

Lande: Well, there are several reasons in general on why to do conservation. These include aesthetic and moral reasons, which is what you have alluded to. This is very important. A lot of fundamentalist religious people, many of whom tend to be politically conservative, now understand that they should be protecting the environment. Even if they don't believe in evolution, they feel they should protect God's creation. But there are very practical reasons as well.

Which are?

Lande: The most practical reasons are first that many modern medicines are derived from natural compounds found in species that most people would not otherwise care about. Second and ultimately, is that functioning ecosystems are what human civilisations depend on. Collapse of some previous civilisations was because they depleted their resources and destroyed their environment. If human civilisation is going to continue at anything like the level of luxury and resource availability that advanced civilisations have now, we must be able to sustain the ecosystems, on which we depend. I think we now are beginning to understand this but there is still a huge uncertainty about how these systems work, making it easy for lawyers and politicians to promote or allow their degradation and destruction. The prudent thing to do is to preserve the main operation of the ecosystem.

You received other awards in your career. What does this Balzan Prize mean to you?

Lande: It does make a huge difference. They were all important recognitions and helped to justify my approach. I was always doing what I wanted to, thinking what I wanted to and not conforming to popular trends.

My own priority has always been on research. Professors are generally encouraged to do equal amounts of teaching, research and administration. I have always placed a top priority on original research. I think I have been an adequate teacher but I have often been chastised for being unpopular with many students. I have always been stimulating to the best students, who are the ones I wanted to reach, and the lazy students didn't like what I did because I didn't spoon-feed it to them. That isn't the way that the trend is these days.

I never had a formal course in genetics nor a formal course in statistics. But I became well known for my contributions to statistical genetics. If you are too highly trained, you're stuck in traditional ways of thinking and it's difficult to break out. Fortunately for me, the people that supervised me from early on, taught me to think independently and to decide for myself what was important. They gave me a great deal of freedom to develop my own ideas.

"Applied science, like conservation, still has a bad name among a lot of pure scientists, who think you shouldn't do anything that is political and you should never advocate anything."

Receiving these awards was a vindication of the disagreements and almost punishments that I got along the way that I rebelled against. Theoretical biology had a bad name among a lot of empirical scientists. Applied science, like conservation, still has a bad name among a lot of pure scientists, who think you shouldn't do anything that is political and you should never advocate anything. I completely disagree with that. Scientists are citizens they have a perfect right to advocate their point of view, as long as they are not biasing the scientific evidence and principles. Otherwise, who is going to speak up for nature, except well-intentioned environmental activists who often don't know how to direct their energy effectively?

Do you think receiving the prize will advance the cause of conservation?

Lande: Yes, I think it does. The Balzan foundation was one of the first foundations that recognised the importance of ecology and evolution. These areas can never receive the Nobel Prize.

In what topic will you invest the research part of the prize? Any hot topic?

Lande: The guidance they give is that you should use the money to support someone in the early stage of their research career. I will be helping graduate students and postdoctoral researchers to understand my work and to continue with original contributions to the theory and applications in evolution, ecology and conservation.

Maybe just an idea of a specific topic?

Lande: Well, the area I got my current job with the Royal Society for is to integrate theories of ecology and evolution. Specific subjects are difficult to predict in advance; other than that nearly everything is potentially important to a species on the brink of extinction.

Interview: Florian Fisch