Q & A

Hopi Hoekstra

Hopi Hoekstra grew up in California but recently moved east to become the John L. Loeb Associate Professor of Biology in the Department of Organismic and Evolutionary Biology and the Curator of Mammals at the Museum of Comparative Zoology at Harvard University. She studies the genetics of adaptation in mammals — both in the lab and the field.

What's with the first name? When I was born, there was some disagreement between my parents about what to call me. However, my Dutch grandmother avoided taking sides and simply referred to me as the '*Hopje*' — a little Dutch candy. By the time my parents agreed on a name, it was too late, and I was already thought of as the little Hopi. My official name, however, is Danielle Elisabeth Hoekstra.

You are a Curator of Mammals, what does a Mammal Curator do? I head the mammal collection at Harvard's Museum of Comparative Zoology (MCZ). The collection comprises specimens collected as early as the 1830s, the red squirrel series collected by Louis Agassiz (one of Darwin's biggest foes), and hundreds of type specimens, including that of *Gorilla gorilla*. I have a terrific staff that looks after the department's day-to-day activities, such as processing research loans and curating new specimens. My primary responsibilities are to develop strategies for the collections (e.g., maintaining a repository of genetic materials, adding more population sampling) and to help develop public exhibits for the museum. My favorite unofficial curatorial duty is giving special guest tours of the attic: armed with flashlights, we can explore the creaky floors and dusty corners crammed with hippopotamus skulls, hundreds of mounted horns and antlers, and the giant ribs of a blue whale.

What turned you on to biology? My mother often asks me this very question, as if she has no idea. I have vivid memories of hiking with her in the Stanford hills near our house where she would collect owl pellets, which we would bring home to dissect and rearticulate the mouse skeletons bone by bone. This was my regular weekend childhood art project. Then, when I went to college at UC Berkeley, two things happened. First, I started doing research in Bob Full's lab, which largely involved running cockroaches on teeny cockroach-sized treadmills. While not the most glamorous of projects, I really was excited by discovery itself — learning new things that no one else in the entire world knew, like how fast a cockroach could run on a treadmill that was right-side-up compared to one that was upside-down... it turns out, there is not much of a difference. Second, I enrolled in a natural history course, taught by three amazing naturalists: Jim Patton, Harry Greene and Ned Johnson. Every weekend we had a field trip, which involved getting up each Saturday morning. Ugh. But, I saw bobcats and rattlesnakes and gophers and newts, and I never missed a trip. My interest in biology clearly started with organisms. I didn't pick up a pipette until I was in graduate school.

Do you have a 'scientific hero'? In the field of evolutionary genetics, Allan Wilson, a true 'Big Thinker,' is under-appreciated. I never met him, but I've been hugely influenced by his work. He was always keen to apply the newest molecular tools to big evolutionary questions. While best known for his work on human evolution, he also spawned an entire generation of molecular ecologists. This includes my Ph.D. supervisor Scott Edwards (making Wilson my academic grandfather), who, in the Wilson tradition, uses cutting-edge genomic technology to study avian evolution.

What is the best advice you have been given? There is one conversation that I had with Bill Rice that has really stuck with me. He reminded me that our academic careers are quite short — something like 30 years of independent research. That's roughly six NIH grants. His advice was thus to choose research projects carefully — ideas are not limiting — and to invest time and effort into work that will both move the field forward and get you really excited.

And what advice would you give? Three points. First, read and think broadly. I would argue that many of the big questions were first posed almost a century ago, and now we are able to answer those questions in ways that were unimaginable. Take the time to read the historical literature: for evolutionary biologists this includes Darwin, Wright, Fisher (if you can), Dobzhansky and Mayr. Second, be prepared and be flexible. For example, my postdoc Heidi Fisher spent hours watching sperm and kept seeing the sperm cells clump together. This had been seen before and was known to increase swimming speed, but she began to wonder if a sperm 'knows' which sperm it should stick to. She designed a simple experiment and demonstrated that sperm can indeed discriminate and preferentially cooperate with closely related sperm. So, don't underestimate the power of observation. Sometimes the most exciting findings come when you least expect them. Third, hard work can get you a long way.

Hopi Hoekstra at the museum. Photograph: Bear Cieri.

Any issues in scientific funding you feel strongly about? Yes. 'Young Investigator' grants and awards can make a huge difference to a nascent career. They are risky, of course, yet they are important and give one the freedom to follow new ideas and take some chances. Now, of course, I wish there were more such awards for mid-career scientists!

What was your favorite conference? *'Evolution —* The Molecular Landscape', a Cold Spring Harbor Symposium celebrating the Darwin bicentenary. It lasted six days, and the talks often went to 11p.m.; it was exhausting, presentations were all first-rate, but best were the interactions before, between and after the sessions. And, it was an energizing mix of disciplines from paleontology to the origins of life to evolutionary genetics and philosophy. The lobster dinner wasn't bad either.

What is your favorite book? It is hard, no impossible, to name one favorite. But, I recently read *Francis Crick: Discoverer of the Genetic Code* by Matt Ridley on a trans-Atlantic flight. It read, as one reviewer put it, "like a guilty pleasure." It was intriguing to learn more about the man behind the science.

Where is evolutionary biology heading? Evolutionary biology is in large part about reconstructing the past. One of the things I am excited about is our increasing ability to do just that with true genetic precision. For example, by identifying mutations that affect phenotypes, we can start to reconstruct traits of extinct species. Already, using phylogenetic methods, we can reconstruct ancient opsin-gene sequences to learn about dinosaur vision. Using ancient DNA, we now know some Neanderthals were red-headed, and some mammoths were blonde. Now imagine reconstructing or sequencing whole genomes and being able to predict the morphology, physiology or even behavior of ancient creatures! To what extent this will be possible is still unclear, but if we have reliable data, we can properly understand the direction and nature of evolutionary change in an unprecedented way. That, surely, is the ultimate goal of our field.

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Quick guide

Levels of selection

Samir Okasha

What is the 'levels of selection' question about? It's about the level of the biological hierarchy at which natural selection acts, e.g. individual, group, gene, community, species, etc. Usually when we think about selection, we think of it acting at the level of the individual organism, favouring the fittest individuals over the less fit and thus leading to evolutionary change. But individual-level selection is only one possibility among many. For the key requirements of evolution by natural selection — variation, associated differences in fitness and heritability — can in principle be met by entities at many levels, above and below that of the individual organism. For example, a selective process could quite easily operate on groups of organisms, favouring some types of groups over others. This idea is known as 'group selection'.

What is the origin of the levels of selection debate? Like much in evolutionary biology, it traces back to Darwin. Though Darwin primarily discussed individual-level selection, he was aware of other possibilities. In *The Descent of Man* (1879), he tackled the problem of how self-sacrificial and other 'altruistic' behaviours could have evolved in early hominids. As such behaviours reduce an individual's fitness, it is clear that they cannot have evolved by selection at the individual level. Darwin suggested that group selection may be the answer. Groups in which altruistic behaviour was prevalent may have enjoyed a selective advantage over groups in which it was absent, he argued. Another early evolutionist who discussed the levels question was August Weismann, mainly in relation to selection at the sub-organismic level. However, the modern debate only really took off in the 1960s with the rise of social evolution theory, and the ensuing controversy over group selection.

Why did 'group selection' become such a chequered concept in the 20th century? Primarily due to George C. Williams' trenchant critique; also influential was the work of John Maynard Smith. They argued that group selection was theoretically possible but unlikely to be a major evolutionary force, and was not needed to explain the known biological phenomena anyway. Also, they stressed the fallacy of assuming that selection on individual organisms would automatically lead to outcomes that benefit the group. This fallacy was surprisingly common in mid-20th century biology and is still encountered today. The rise of 'kin selection' also contributed to the demise of group selection. Biologists such as Richard Dawkins and John Maynard Smith argued that kin selection or inclusive fitness theory, first articulated by William D. Hamilton in the 1960s, provided a better explanation of phenomena such as altruism which had traditionally been taken as evidence for group selection. However, the true relation between kin and group selection is a controversial matter. Many modern theorists argue that suitably understood they are in fact *equivalent*, so do not constitute alternative scientific hypotheses at all.

But isn't the gene the real unit of selection? Dawkins originally presented his 'selfish gene' idea as an empirical alternative to individual and group-level selection, but later realised the error of his ways. Almost any selection process, at any level, will ultimately lead to a change in gene frequencies, so can be described as a process in which one gene spreads at the expense of its alleles. Thus, it is generally wrong to contrast 'gene selection' with either individual or group selection — there is no empirical issue at stake here. This was the point that Dawkins later captured with his 'replicator–vehicle' distinction; others have marked it by contrasting *units* and *levels* of selection. In recent literature, 'gene-level selection' is often used in a restricted sense, to mean selection between genes within a single organism, as occurs in cases of intra-genomic conflict, e.g. meiotic drive. In this sense, most selection processes cannot be described as gene selection.