High-altitude Adaptation in Rufous-collared Sparrows

By Zachary Cheviron, Ph.D., Postdoctoral Scholar, Center for Tropical Research, Institute of the Environment, UCLA

The ways in which species cope with harsh high-elevation habitats are classic examples of adaptation in nature. Perhaps most famous are the studies of hemoglobin variation in high-elevation birds and mammals. Bar-headed Geese (*Anser indicus*), for example, routinely migrate over the peak of Mt. Everest on their way to breed in wetlands high in the Himalayas. These geese possess hemoglobin molecules that bind oxygen much more tightly than those of their relative, the Graylag Goose (*Anser anser*), that breeds at low elevations. This difference is due to just two well-placed mutations that dramatically alter the ability of hemoglobin molecules to bind oxygen. Small genetic changes have also been shown to alter hemoglobin in deer mice (*Peromyscus maniculatus*). Studies of other species, however, have shown that variation in many other physiological traits are important in dealing with high elevation and that hemoglobin variation is just one route up the high-altitude adaptive peak.

For the past six years, I have been studying the genetics of high-altitude adaptation in the Rufous-collared Sparrow (*Zonotrichia capensis*) in the Peruvian Andes. Rufous-collared Sparrows have one of the largest elevational distributions of any songbird in the world. If you are birding in Peru, you will undoubtedly spot this bird in virtually every kind of open habitat – singing in a city park at sea level in Lima, perched on an agave in the arid montane scrub of the western Andean slope, or foraging in the puna bunch grass at 4,500 meters above sea level high in the Andes. These sparrows are ubiquitous and continuously distributed along the entire length of the elevational gradient.

*Typical Rufous-collared Sparrow (*Zonotrichia capensis*) habitats along an elevational gradient on the western Andean slope in the Peruvian Andes. Left: Agricultural fields along the coast (100 m). Middle: Arid montane scrub (2,000 m). Right: Puna grassland (4,200 m).*

As anyone who has spent time at high elevation can attest, environmental conditions change drastically along elevational gradients, and the gradient that Rufous-collared Sparrows inhabit is no different. At the highest elevations, mean minimum daily temperature is roughly 18º Celsius colder than it is on the coast, and there is also about a 40% reduction in the partial pressure of oxygen. In this part of its range, Rufous-collared Sparrows are non-migratory, so they must endure these conditions year-round. These environmental conditions result in selective pressures that differ among altitudinal environments. Physiological studies performed in the early 1990s showed that high elevation populations had significantly greater cold tolerance than coastal populations. Interestingly, however, the two populations did not differ in hypoxia tolerance. These experiments suggested adaptation of high- and low-elevation populations to their local temperatures, but nothing was known about the genetic basis of these traits or how these physiological differences could be maintained in the face of gene flow along the elevational gradient.

As a beginning graduate student at the Louisiana State University Museum of Natural Science, I decided that making steps towards filling in those gaps would make an interesting dissertation project. The first step involved collecting population samples along a series of transects in Peru. I designed a sampling regime that consisted of replicate elevational test transects and latitudinal control transects. The elevational transects spanned a dramatic increase in elevation over a relatively short geographic distance, whereas the control transects spanned a much greater distance over a relatively uniform elevation. This sampling design allowed me to separate the effects of distance from elevation. Using this sampling design, I first estimated levels of gene flow along each transect for several genes. Comparing levels of gene flow among several genes can help to identify those that are under selection in different habitats – alleles at neutral genes should move easily between habitats, whereas selection should reduce gene flow at genes involved in adaptation.

Two high-elevation field sites in the central Andes during different seasons. Left: Outside La Oroya, Peru (4,100 m) in June. Right: Near Lircay, Peru (4,300 m) in February. Rufous-collared Sparrows are non-migratory in this portion of their range and this seasonality is added physiological stress for individuals living at high elevation.

In general, levels of gene flow were very high for all of the genes except those encoded by the mitochondrial genome. There was a sharp transition in mitochondrial haplotype frequency centered at around 3,800 meters above sea level on both elevational transects. This elevation is significant because it is the point at which average daily minimum temperatures drop below freezing in the winter. The transition in mitochondrial haplotypes was abrupt - occurring over only 10 kilometers, a distance that is well within the sparrows' dispersal capabilities. None of the nuclear genes that I examined showed a similar shift between high- and low-elevation populations. Since there was not a similar mitochondrial pattern along the control transects, these results were not due to peculiarities in the inheritance of the mitochondrial genome.

Instead, these results suggest that genes in the mitochondrial genome may be important in local adaptation. The mitochondrion is the "power plant" for cells, and genes encoded within its genome are essential for metabolism. High metabolic rates are known to be under selection in cold, high-elevation habitats. It is possible that differences in mitochondrial genes influence metabolic rates and different mitochondrial haplotypes would be favored in different altitudinal environments. Earlier this year, I traveled to Peru to collect samples to test for functional differences between the high- and low-elevation haplotypes. These samples will be key to testing this hypothesis.

One unanswered question in the genetics of high-altitude adaptation is the extent to which differences in gene expression play a role in adaptive evolution. To address this question, I used a newly developed genomic tool, a microarray, to measure the expression of thousands of genes simultaneously in high- and low-elevation sparrows that were sampled at their native elevations. Hundreds of genes were differentially expressed, and most of these genes were involved in metabolic processes, including some mitochondrial genes. This variation in metabolic gene expression may underlie the differences in cold tolerance that were documented by physiologists nearly 20 years ago.

Gene expression is highly plastic and can change dramatically over very short periods of time to match local environmental conditions. To examine the degree of plasticity in these expression patterns, I transferred individuals to a common altitude in Lima, Peru. After just one week in Lima, all of the expression differences I saw when birds were sampled at their native elevations vanished! These results demonstrate a high degree of plasticity in metabolic gene expression and possibly metabolic rate as well.

This work has just scratched the surface of what can be learned about high-altitude adaptation in this fascinating sparrow. So far, it looks like the story is complicated, with both genetically encoded differences and phenotypically plastic traits contributing to this species' ability to cope with environmental conditions along this dramatic elevational gradient.

At CTR, I am continuing to work on Rufous-collared Sparrows, and I am extending this work to other bird species in the Andes and the Sierra Nevada. This research will help determine whether these patterns can be generalized to other species and explore how this information can be used to understand how high-elevation species adapt to climate change.

Left: Zachary Cheviron birdwatching with local children on the shore of Lago Titicaca in Chucuito, Peru. Right: An adult Rufous-collared Sparrow.