

Ancient Patagonian rodent DNA provides clues to the evolution of social behavior

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The colonial tuco-tuco (*Ctenomys sociabilis*) has so little genetic diversity that it should have disappeared long ago. Yet the hearty creature has not only managed to survive for thousands of years in the harsh climate of the Argentine highlands, it has evolved a complex social structure that's unique among the more than 50 closely related tuco-tuco species. Courtesy of Yvonne Chan

A rare Patagonian rodent known as the colonial tuco-tuco fascinates biologists because it seems to defy all odds. This threatened species has so little genetic diversity that the slightest whiff of climate change or disease should have wiped it off the face of the earth long ago.

Yet the hearty gopher-like creature has not only managed to survive for thousands of years in the harsh climate of the Argentine highlands, it has evolved a complex social structure that's unique among the more than 50 closely related tuco-tuco species.

Stanford University biologist Elizabeth Hadly and her colleagues are using DNA extracted from ancient teeth—some more than 10,000 years old—to unravel the colonial tuco-tuco's mysterious past and pinpoint the cause of its low genetic diversity.

The results are published in the April 20 edition of the journal *PLoS Genetics*.

"This advance in the analysis is fundamentally different from anything anyone has done with ancient DNA," says Hadly, an associate professor of biological sciences and co-author of the study. "What we're trying to do is basically make a moving picture of their history instead of just a snapshot."

Adopting a colonial lifestyle may have been the key to the rodent's survival, Hadly asserts, and could provide insight into the evolution of social behavior in other animals, including ants and humans.

Population crash

Named for the "tuc-tuc-tuc" sound of its call, the colonial tuco-tuco (*Ctenomys sociabilis*) lives in remote highland savannah areas of southern Argentina. Unlike the more than 50 other tuco-tuco species that live mostly solitary lives, *C. sociabilis* lives in colonies. Several females frequently share one burrow and in captivity are known to nurse one another's young.

Almost entirely subterranean, colonial tuco-tucos rarely leave their burrows except for brief forays to collect the grassy vegetation on which they feed. When they do leave their colonies, the rodents often make a tasty meal for prowling owls. For thousands of years, these owls have roosted in two caves near the Chilean border and regurgitated pellets of indigestible fur, bones and teeth while they rest. From these teeth, scientists can determine which rodent species lived in a roughly 3-mile radius of the cave at any given time.

Using modern and ancient DNA from tuco-tuco teeth found in the two caves, Stanford graduate student Yvonne Chan, lead author of the *PLoS Genetics* study, mapped the rodent population through time. Her results show that over the last 10,000 years, the once dominant colonial tuco-tuco,

C. sociabilis, was gradually crowded out of the northern cave area by a larger species of tuco-tuco, *C. haigi*. Around 3,000 years ago, *C. sociabilis* disappeared entirely from the northern cave site. At the same time, the genetic diversity of *C. sociabilis* in the southern cave declined precipitously.

"When you talk about genetic variation being lost, you need to really reduce [the population] to a small number of individuals," Chan says.

By fitting modern and ancient DNA data into a standard population genetics model, Chan was able to pinpoint the drastic decline of *C. sociabilis* to about 2,600 years ago, when the population was likely reduced to less than 300 individuals. When a population becomes that small, it loses much of its genetic diversity—a phenomenon known as a genetic bottleneck. Chan thinks that a volcanic eruption known to have occurred in the Andes roughly 3,000 years ago, combined with environmental change and competition from the larger species of tuco-tuco, likely caused the die-off.

Most genetic studies rely entirely on modern DNA to estimate historical population size, but Hadly and Chan's technique provides much more detailed information. "You can't get the bottleneck time or the bottleneck size without both modern and ancient DNA," Chan explains.

Social evolution

Determining how the colonial tuco-tuco's diversity got so low only solves part of the mystery. "The really curious thing is how the species managed to persist for around 3,000 years with almost no genetic variation," Hadly says. "Genetic variation is the toolkit for dealing with whatever the environment has to throw at you. If you have only a couple of tools, you don't have a lot of resilience for dealing with an unexpected event."

According to Chan, the evolution of the colonial tuco-tuco's social behavior may be linked to the population bottleneck. Because all surviving colonial tuco-tucos are closely related, it makes sense evolutionarily for individuals to cooperate, she says.

"If you're closely related to everyone, there's not as much reason to fight," Chan explains. "Tucos have a high cost to dispersal—if they leave their burrow they tend to get eaten. If they stay home and help their sisters breed, it makes sense because they'll be helping to pass on genes that are almost identical to their own."

No one knows exactly when social behavior evolved in *C. sociabilis*, but Hadly suspects it was a response to the population crash. "Maybe the evolution of sociality actually confers some advantage to withstanding periods of low genetic diversity," she says. "Most behaviorists would say that sociality is so complicated that it takes a while to evolve, but maybe if a species has to be social to survive, social behavior could evolve pretty rapidly."

If so, the study of rare Patagonian tuco-tucos could have implications for understanding the evolution of sociality in other species that have experienced evolutionary bottlenecks, Hadly says. Population crashes and migration events with a small founding population may have encouraged the rapid development of social behavior in the Argentine ant when it colonized North America, she says, and even in ancient human populations. At the very least, combining ancient and modern DNA with population models will help geneticists understand the role population size and structure play in the maintenance of genetic diversity.

"I think eventually this will feed back into modifying our understanding of population genetic theory and how sensitive it is to real-life events," Hadly explains.

Most of the work conducted in Hadly's lab focuses on using ancient DNA to examine how living species have responded to climate change in the past. With this information, she hopes to gain insights into the way current global warming trends will affect rare and threatened species, such as the colonial tuco-tuco.

"What better way to understand how tuco-tuco populations respond to environmental changes than to look at 10,000 years of their history," she says. "They're the survivors of the last big extinction event, so it seems logical to me that we

should know how they did that."

Former undergraduate student Christian Anderson also co-authored the PLoS Genetics study. Research was funded by the Environmental Protection Agency, the Center for Evolutionary Studies in the Department of Biological Sciences at Stanford and the National Science Foundation.

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