# The Greenbeards Have Blue Throats In The Evolution Of Altruistic Behavior

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A new study of side-blotched lizards in California has revealed the genetic underpinnings of altruistic behavior in this common lizard species, providing new insights into the long-standing puzzle of how cooperation and altruism can evolve.

The study, led by researchers at the University of California, Santa Cruz, offers the first evidence in vertebrates of an important theoretical concept in evolutionary biology known as "greenbeard" altruism.

"This reflects a major breakthrough in our understanding of how cooperative behavior arises from genes," said Barry Sinervo, professor of ecology and evolutionary biology at UCSC and first author of a paper describing the new findings. The paper will be published in the May 9 issue of Proceedings of the National Academy of Sciences (PNAS) and is currently available in the online early edition of PNAS.

The paper describes unrelated male lizards that form cooperative partnerships to protect their territories. These partnerships are often mutually beneficial, enabling both partners to father more offspring than they would on their own. Under some circumstances, however, one male in the pair may have few or no offspring as a result of protecting its partner from the aggressive intrusions of other lizards.

This type of cooperation, in which one individual bears all the costs and another unrelated individual receives the benefits, is called "true altruism." These lizards have an annual life cycle, so this behavior may spell the end of the altruistic male's lineage.

The evolution of cooperation is puzzling because cooperative systems are vulnerable to cheaters or defectors. Cheaters and defectors benefit from the cooperative behavior of others without paying the costs, so they ought to be favored under natural selection. But then cheater genes would spread in the population, and the cooperative system would collapse. The greenbeard effect is one way to get around this.

The concept originated with the British evolutionary theorist W. D. Hamilton and was popularized by Richard Dawkins in his book The Selfish Gene. Dawkins illustrated the concept with a hypothetical example in which a green beard serves as a marker enabling individuals with a gene for cooperation to recognize others with the same gene. The greenbeard gene (or genes) must do three things: establish a signal (the green beard), enable recognition of others that share the signal, and promote cooperative behavior towards other greenbeards.

In side-blotched lizards, the greenbeards have blue throats. This species comes in three different throat colors--orange, yellow, and blue--and throat color corresponds to different territorial behaviors in the males. Blue-throated males form partnerships in which two males cooperate to protect their territories; orange-throated males are highly aggressive and usurp territory from other lizards; and yellow-throated males sneak into the territory of other males to mate with females.

Previous research by Sinervo and his collaborators has demonstrated that these strategies result in a kind of "rock-paper-scissors" game in which orange defeats blue, blue defeats yellow, and yellow defeats orange. The lizard populations go through cycles in which one color after another increases its numbers at the expense of the others, but none are able to maintain dominance.

In the new paper, Sinervo's group investigated the genetic basis of the cooperative behavior in blue-throated males. They found that, in addition to the gene that controls throat color, there are at least three other genetic factors that determine the components of the greenbeard effect.

"Our study provides the first comprehensive genetic evidence of a greenbeard in vertebrates," Sinervo said. "Unlike Hamilton's idea and most modern views of greenbeards, we find that many genetic loci across the genome 'cooperate' to establish conditions for the greenbeard behaviors."

The cooperative behavior of blue-throated males plays out differently depending on the frequency of aggressive orange males in the population. In years when there are few orange males, cooperating blue males both benefit. But when orange males are common, one blue male ends up serving as a buffer for his territorial partner, bearing the brunt of the advances of aggressive orange males. Thus, the behavior of the blue-throated males cycles between mutualism and altruism, depending on where the population as a whole is in the rock-paper-scissors cycle.

"One of the big problems in the evolution of altruism is explaining how it gets off the ground in the first place," said Alexis Chaine, a graduate student in ecology and evolutionary biology at UCSC and a coauthor of the paper. "This is a situation that oscillates between mutualism and altruism, depending on the circumstances. Periods of mutualism give a much-needed boost at early stages in the evolution of altruistic genes and also provide long-term stability to the cooperative relationship."

"True altruism may be something that is evolutionarily fleeting, and what keeps it stable is the long-term payoff," Sinervo added. "The lizards are in a bind. They can't break up the partnership, because the success of the blue strategy depends on cooperation. Evolution has set them up so they can't cheat and turn on their partner."

The study is the culmination of two decades of laboratory and field research by Sinervo's lab to develop a deep pedigree of side-blotched lizards and their behavioral traits in the field. The researchers have tracked 18 generations of lizards so far and have mapped the locations of genes that coordinate reproductive behavior and throat color, as well as "genetic self-recognition"--the ability to recognize other individuals with the same gene complex.

The researchers used genetic tests to determine the paternity of all the lizards in each generation, and from this they could determine the "fitness" of each male in terms of the number of offspring he fathers. The fitness of altruistic blue males drops to nearly zero, while the protected partner is able to maintain high fitness. But in years when orange males are few, both blue males in a partnership have high fitness. Sinervo emphasized that the cooperative blue males are not even remotely related to one another.

"All other examples of greenbeards are found in invertebrates, such as ants, or lower taxa, such as slime molds, and in all these examples the researchers have not completely ruled out the confounding effects of kin selection," he said. "We establish that the greenbeard of the side-blotched lizard is not confounded by the effects of kin-helping behavior."

Interestingly, not all blue-throated males possess the complete set of genes required for greenbeard altruism. These "loner males" do not form partnerships with other blue-throated males. Their fitness is higher than that of altruistic males, but lower than that of the protected partner. And in years when blue-male partnerships are mutually beneficial, the fitness of loner males is lower than that of cooperating males.

The existence of loner blue males means that the genetic self-recognition required to establish a partnership involves more than the recognition of a blue throat in the other male. Cooperative males are able to recognize others that possess the complete set of genes for cooperative behavior.

"These are genes that cause lizards to recognize one another at the gene level and cause them to act in a certain way. The genes are driving the whole social system," Sinervo said.