

# Natural selection for moderate testosterone surprises scientists

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The relationship between testosterone and evolutionary fitness is more complex than scientists thought. Credit: Jonathan Atwell

A field study of the relationship between testosterone and natural selection in an American songbird, the dark-eyed junco, has defied some expectations and confirmed others.

Scientists from Indiana University Bloomington, the University of Virginia, Indiana University-Purdue University Indianapolis, and the University of Southern Mississippi report in the June issue of [The American Naturalist](#) that extreme testosterone production -- high or low -- puts male dark-eyed junco at a disadvantage in both survival and reproduction outside their semi-monogamous breeding pairs. The results are based on a wild population of juncos studied near the University of Virginia's Mountain Lake Biological Station.

"Our goal in this study was to characterize natural variation in testosterone production in the wild and to learn how that relates to natural variation in survival and [reproductive success](#)," said Joel McGlothlin, a Virginia postdoctoral fellow who conducted the project as an IU Bloomington Ph.D. student. "We learned there are far more complex things going on here than we expected."

Past studies of juncos (and other animals) have shown that testosterone presents something of a trade-off, by exerting opposing effects on survival and reproduction in wild populations. High testosterone is often associated with aggression in male animals and sometimes with suppressed immunity. These effects can harm a male's chances of survival but also yield more opportunities for him to mate. Low testosterone production is presumed to have the opposite effect -- increased survival and fewer mating opportunities.

But that isn't what members of IU Bloomington Distinguished Professor of Biology Ellen Ketterson's research group saw.

Instead, they saw "stabilizing selection" on testosterone production when looking at both survival and reproduction. The male juncos that were most likely to survive produced intermediate levels of testosterone. Likewise, the male juncos that produced the most offspring were also more likely to produce moderate levels of testosterone. High and low testosterone production, on the other hand, were associated with failure in both survival and reproduction.

The current *American Naturalist* study argues that natural selection is favoring intermediate testosterone levels in the population of male juncos the scientists examined, and because testosterone-mediated behaviors are often inherited, the prediction is that moderation will prevail over time.

"As for why, we don't know for sure what's going on yet," McGlothlin said. "We expected that high testosterone would lead to lower survival rates, and that's what we observed. But it's not clear why low testosterone also led to lower survival rates. We would have expected the opposite. We have some ideas, and that's something we're going to investigate soon."

Employing a great deal of student help, the scientists mapped out all junco nesting sites in their study area. From spring to fall, the researchers caught [males](#) multiple times. Immediately after capture and prior to release, the juncos were given a gonadotropin releasing-hormone "challenge," which causes the birds' bodies to produce testosterone. Past studies have shown the levels of testosterone induced by the challenge are proportional to the birds' natural tendency to produce testosterone in response to a rival in the wild. The challenge therefore gives scientists a sense of what levels of testosterone production are normal for each bird.

The researchers also collected DNA samples from the males and their mates. They then visited each nest and collected DNA from the nestlings. Comparisons of the male genotypes with offspring genotypes revealed paternity and told the scientists just how successful each particular adult male junco was at reproducing. Juncos are semi-monogamous in that males pair and nest with a particular female, but often attempt to mate with females mated to other males.

"We were able to pick apart what was going on there," McGlothlin said. "By splitting reproduction into two different components, we were able to see how successful male birds were at home versus how they did away from home."

After tallying within-pair and extra-pair matings, the scientists produced two more unexpected results. Higher testosterone was associated with more offspring from within-pair matings, and intermediate levels of

testosterone were associated with more extra-pair offspring.

"Which may seem counterintuitive," McGlothlin said. "We think what's going on is a time trade-off. For a male to make sure he is fertilizing the offspring in his home nest, he must spend a fair amount of time near his nest and perhaps follow his paired female around to make sure no other males approach her. Testosterone makes males more territorial and more likely to engage in that behavior."

Low testosterone levels were shown by McGlothlin, Ketterson, and others in 2007 to cause males to spend more time parenting offspring in their nests, but also to be less territorial. McGlothlin said that might explain why his group saw a balancing effect for testosterone on extra-pair offspring. Males with low testosterone may make fewer forays to other nests, reducing their likelihood of encountering other males, while those with very high testosterone may be staying home for a different reason -- to guard their territory against potential intruders. Alternatively, these high-testosterone males may be seeking extra-pair mates, but are unsuccessful, perhaps because the behavior they produce is unattractive to females.

In evolutionary biology, the fitness of an individual organism is dependent on its capacity for survival and reproduction, but it is also a relative thing -- for any given character, fitness depends on how one set of genes or attributes performs in relation to all the other individuals in a population. This study suggests that when it comes to testosterone and the behaviors it controls, moderation helps provide this competitive edge.

"These findings represent the culmination of 20-plus years of research directed towards understanding how variability in male testosterone relates to Darwinian fitness, and the outcome is deeply satisfying," said Ketterson, a principal investigator and coauthor. "Initially we took an

experimental approach, which revealed that chronic elevation of testosterone reduced lifespan in the junco. But the story could not be complete without knowing whether males with naturally high or low levels of testosterone were at a survival advantage or disadvantage. Much of the literature on testosterone suggests that more is better. Our studies, experimental and correlational, now show that while 'high-T males', as we call them, may sometimes benefit in reproduction, too much [testosterone](#) leads to lower survival, and it's the average male that is the best performer."

**More information:** "Natural Selection on Testosterone Production in a Wild Songbird Population," *The American Naturalist*, v. 175, no. 6, by Joel W. McGlothlin et al

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