

## 'War Between the Sexes:' The Co-evolution of Genitalia in Waterfowl

May 1 2007

A team of biologists at Yale University and the University of Sheffield discovered anatomical details about the female reproductive tract in waterfowl that indicate that male and female anatomy have co-evolved in a "sexual arms race."

In most birds, copulation consists of a simple, and rather chaste, "cloacal kiss." But, avian diversity includes a few ancient lineages that retained the grooved phallus found in their reptilian ancestors. Among living birds, the waterfowl are one of the lineages that still have the phallus. Waterfowl are also distinct in having great diversity among different species in the length and ornamentation of the phallus.

This diversity in waterfowl phallus size and shape has been previously explained as a result of sperm competition. Scientists speculated that sperm from males with a longer phallus had a competitive edge over sperm from those less well-endowed. This report in the online journal PLoS ONE shows that there is a lot more to the story.

"As part of a research program on the evolution of the avian phallus, I was curious to know if there were consequences to female ducks of the tremendous anatomical variation found in the male phallus," said lead author, Patricia Brennan, a joint post-doctoral researcher in Ecology and Evolutionary Biology at Yale and Animal and Plant Sciences at University of Sheffield, UK.

Her study is a complementary exploration of the anatomy of the female



reproductive tract, called the oviduct or vagina, which is usually very simple and similar among birds. Brennan found two unexpectedly complex and entirely novel structures that all seem designed for one purpose — to selectively exclude the male phallus.

In most birds, the oviduct is a simple tube, but in some waterfowl, the tube has unique sacs and spirals. The sacs are out-pocketings in the sides of the tube that are just inside the opening of the oviduct. "They appear to function as 'dead-ends,' or false passages," said Brennan. "If the phallus were to enter one of these sacs, it would not progress further into the oviduct where it would deposit sperm more effectively."

The second structural novelty of the female is a series of tight, clockwise spirals in the tubular oviduct. "Interestingly, the male phallus is also a spiral, but it twists in the opposite, counter-clockwise, direction," says Yale ornithologist and co-author Richard Prum. "So, the twists in the oviduct appear designed to exclude the opposing twists of the male phallus. It's an exquisite anti-lock-and-key system."

The number of sacs and spirals in the reproductive tract of various female waterfowl correlates strongly with the length of the male phallus. Comparing the phallus size and oviduct shape in 14 different species of ducks and geese, the authors show that the genitalia of males and females have dynamically co-evolved with one another.

According to the study, in various independent lineages of ducks females developed more elaborate oviducts as males evolved longer phalluses. In other lineages females lost oviduct complexity as the phallus evolved toward smaller size.

Why all this dynamic evolution? Brennan hypothesizes that the female waterfowl have evolved these unique anatomical features as physical counter-measures to evade male attempts to assert control over



reproduction. "Despite the fact that most waterfowl form monogamous pairs, forced copulations by other males — the avian equivalent of rape — are common in many waterfowl," said Prum. "The length of the phallus of a species is strongly correlated with the frequency of forced copulations."

"In response to male attempts to force their paternity on females, female waterfowl may be able to assert their own behavioral and anatomical means of controlling who fathers their offspring," Brennan said.

Consequently, the authors propose that elaborate phalluses and female oviducts have co-evolved in a dynamic response to one another. Phalluses that are more elaborate have selected for improved means of excluding them, and vice versa.

What happens when a female duck wants to mate with its chosen partner? The authors speculate that these physical barriers are easily overcome when females cooperate during copulation, and that they only function to exclude unwanted advances.

Brennan is pursuing these results with further exploration of the development and evolution of genitalia in birds. "I am sure there are more surprises out there," she said! Her further research will ask why different lineages of ducks and other birds vary in breeding biology and genital complexity.

Source: Yale University

Citation: 'War Between the Sexes:' The Co-evolution of Genitalia in Waterfowl (2007, May 1) retrieved 26 April 2024 from <u>https://phys.org/news/2007-05-war-sexes-co-evolution-genitalia-waterfowl.html</u>



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