

**Annotated Bibliography: How Did Sexual Conflict Drive the Evolution of Waterfowl
Penises?**

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The role of female investment in a sexual arms race

Leisler, Bernd, and Hans Winkler. "The Role of Female Investment in a Sexual Arms Race."

Journal of Avian Biology 51, no. 5 (2020): jav.02322. .

Male waterfowl, specifically ducks, conduct promiscuous forced copulations with females, leading researchers to question the corkscrew morphology of both male and female sex organs. Such an irregular morphology has prompted research into the evolutionary background of not only these shapes, but also male tendency to engage in forced copulations. Past research has concluded that increasing penis size positively correlates to forced copulation frequencies. This has sparked the hypothesis that females have evolved complex vaginal morphologies to contradict the male copulations. This paper poses the question- do females provide a greater investment in eggs to match larger penis sizes of males? The argument that penis size and egg size may be correlated does not have sufficient evidence to prove the correlation, hence why the hypothesis was rejected upon experimentation. In accepting the hypothesis, this would assume that females see a connection between impressive penises and larger offspring, which seems too superficial, even for ducks. This theory does not hold as embryonic morphology cannot correlate to female behavioral choices. This is supported by the negative correlation found between egg size and phallus size. A more effective study would compare behavioral traits separately from biological processes, for example, exploring the relationship between egg size and growth rate of ducklings. This study supports my topic question by providing gaps in the literature regarding the characteristics of waterfowl phallus evolution.

Coevolution of Male and Female Genital Morphology in Waterfowl

Brennan, P. L., Prum, R. O., McCracken, K. G., Sorenson, M. D., Wilson, R. E., & Birkhead, T.

R. (2007). Coevolution of Male and Female Genital Morphology in Waterfowl. *PLOS ONE*, 2(5), e418. <https://doi.org/doi:10.1371/journal.pone.0000418>

Reproductive organ complexity was compared intraspecifically and interspecifically to classify covariation distinctions in the waterfowl. Two species that do not force copulations and as a result, have simple genitals, were used as controls. Reproductive organs from both male and female ducks were collected throughout the reproductive season from mating pairs of 16 waterfowl species. Measurements were collected from the phallus, testes, ovaries and vaginas of respective ducks. Two new anatomical features were discovered in waterfowl female genitalia: dead-end sacs, and clockwise coils. These features work to exclude the introduction of the male penis during copulation. This evidence was charted within the phylogenetic tree to examine the trends in waterfowl penis length. Measurements were separated into three phallus length classes, and along the cladogram, showed variation within the species lineages. The data concluded that there is a positive correlation between phallus length and vaginal complexity. This is evidence for the coevolution of genitalia in numerous waterfowl species. Because waterfowl can copulate in the water, these spirals of the vagina could have been used as a mechanism to prevent water contamination of the copulation, however, this hypothesis cannot explain why the vagina is twisted in the opposing direction to the male's penis. Other water-copulating species, such as the crocodile, lack these spirals present in waterfowl. This paper provides a strong method of analysis into the complicated history of coevolutionary trends of waterfowl genitalia. The

presentation of cladistic analysis, phallus to vaginal complexity correlation, and comparison to species with absence of forced copulation provide the necessary argument to validate the hypothesis of coevolution of genitalia via sexual conflict in waterfowl species. This study provides evidence to the coevolution of genitalia complexity within waterfowl, overall supporting my research in the fact that females have coevolved antagonistic morphologies to counteract male forced copulations in select species.

Sexual selection and the intromittent organ of birds

Briskie, James V., and Robert Montgomerie. "Sexual Selection and the Intromittent Organ of Birds." *Journal of Avian Biology* 28, no. 1 (1997): 73. <https://doi.org/10.2307/3677097>.

Few species of extant bird species still retain the male intromittent organ (penis), some being ducks. Two new hypotheses by Briskie and Montgomerie suggest that male intromittent organs are favoured when parental investment increases as it may increase a male's confidence during copulation. On the other hand, the loss of male phallus' may be due to female preference to the absence of the organ. The viability of this hypothesis holds as females that are not fertilized by a phallus lay smaller, less costly eggs than species that use a phallus for internal fertilization. Using a phallus for internal semination is more efficient and successful than using only genital contact between breeding sexes. There is a benefit of internal copulation to male ducks, being that it allows them to place sperm high in the female's reproductive system and increase male confidence. To females however, creating more elaborate vaginas helps form female choice in terms of genital rejection during copulations, especially if the copulation is between species where males do not possess an external penis. Briskie and Montgomerie's paper

does not include any experimental evidence, rather, compares the leading hypotheses within this niche. The hypotheses are supported by other research studies and provide adequate reasoning and methodology to support the validity of the argument. This article is relevant to my research as it provides a basis to the theories surrounding the evolutionary reasoning for the presence of intromittent organs in waterfowl, while most birds have lost them throughout the process of natural selection.

Intromittent Organ Morphology and Testis Size in relation to Mating System[s] in Waterfowl

Coker, Christopher R, et. al. *INTROMITTENT ORGAN MORPHOLOGY AND TESTIS SIZE IN RELATION TO MATING SYSTEM IN WATERFOWL*. *The Auk* 119(2):403–413, 2002.
<https://doi.org/10.1093/auk/119.2.403>

If female waterfowl prefer males that do not use forced copulation methods, why hasn't the intromittent organ disappeared through sexual selection? This paper by Coker et al., explores the morphological variations of phalluses in male waterfowl while questioning their relation to mating strategies. Measurements of length and weight were taken from drawings of the male phalluses from 54 species. Circumferences and ridge amounts were taken at random locations along the organ, among other ridge and knob measurements. Measurements were also taken from testes collected from 44 of the examined species through means of museum preservations and literature. The theory that the intromittent organ may prevent water damage to sperm is one that cannot explain the diversity within phallus morphologies throughout waterfowl species.

Waterfowl that use forced copulation strategies typically have larger penises with larger surface areas covered with prominent ridges and/or knobs. If waterfowl used larger intromittent organs for confidence, then this would not support the fact that organ sizes have a positive correlation with increased use of forced copulations. It is suggested that since males must catch females for forced copulations, larger penises attribute to more success mating as the female cannot remove the organ as easily. Male waterfowl that perform forced copulations were found to have larger testes and intense sperm competition. This led to the conclusion that larger intromittent organs are also related to sperm competition intensity. The theories suggested in this paper seem most plausible when compared with the other current theories regarding the morphologies of male phalluses in waterfowl. The methods in this paper, however, use illustrations drawn to scale from museum preserved specimens. Illustrations do not provide the accuracy of specimen extraction and therefore could demonstrate incorrect evidence in conclusions. A stronger argument could be made using sampled evidence with precise measurements instead of preserved specimens, in turn creating more accurate results using up to date specimens. This article is relevant to my research topic as it describes alternative methods of measuring intromittent organs in waterfowl and provides more reasonable theories into the evolution of intromittent organs in waterfowl.

The Effects of Sperm Competition on Testes Size and Intromittent Organ Morphology in Waterfowl

Coker, Chris R. "The Effects of Sperm Competition on Testes Size and Intromittent Organ Morphology in Waterfowl." *University of British Columbia*. (1998). doi: 10.14288/1.0088514

Extra-pair copulations (EPCs) refer to matings with other birds outside a couple's mating bond. This paper examines the relationship between morphology of intromittent organs (testes and penises) and sperm competition through frequency of EPCs. Data were collected from museum and literature specimens killed during the breeding season. Sperm competition was classed by species into 4 categories ranging from monogamy to promiscuity. Results found that testes mass increased with the frequency of EPCs. Moreover, testes possess a significant positive relationship with phallus size within the 57 species in this study. This evidence can support the idea that males with bigger testes are capable of performing EPCs more frequently. Additionally, evidence suggests that the intromittent organs evolved independently from the body size of waterfowl, meaning it evolved on another basis apart from body size competition. Limitations in this study also include the fact that preserved museum specimens were used as samples, and only one specimen per species were used. The disuse of replicates may not represent an accurate sample of the population's intromittent organ features resulting in skewed results and creating bias. Another limitation may be the use of illustrations from museums as accurate forms of specimens. Drawings are archaic forms of method collecting and may not include all features of the organs. This study is relevant to my research as it provides many insights to relationship trends between morphologies.

Explosive eversion and functional morphology of the duck penis supports sexual conflict in waterfowl genitalia

Brennan, Patricia L. R., Christopher J. Clark, and Richard O. Prum. "Explosive Eversion and Functional Morphology of the Duck Penis Supports Sexual Conflict in Waterfowl Genitalia." *Proceedings: Biological Sciences* 277, no. 1686 (2010): 1309–14. doi:10.1098/rspb.2009.21

Forced copulations occur in waterfowl and conclude in sexual conflict between the sexes as a means of control of fertilization. This fight for control has seemingly influenced coevolution of genitalia within these waterfowl species. Females have pocketed vaginas with vaginal spirals opposing the corkscrew-shaped penis of males. Few differences are seen within the functionality of the penis in comparison to primates, one being that during eversion, the male waterfowl's phallus emerges due to the lymphatic system, not the circulatory system. Due to lymphatic control, the male can evert his penis in seconds. This study used high-speed cameras to film and measure maximum eversion while the male was mid- ejaculation. Eversion was measured into a tube, shapes of which consisted either of straight, clockwise spiral, counterclockwise spiral, and a 135-degree angle to simulate the angle of a female. The speed of eversion was measured against that of the straight tube. Experimental evidence showed that clockwise spirals and 135-degree angle to the male's counterclockwise spiral penis present significant mechanical barriers to the full eversion of the penis. The combination of the counter-spiraled vagina and 135-degree angle together would successfully prevent deep deposit of sperm, therefore decreasing the likelihood of fertilization by a male. The authors however, observed new female behaviors that suggest there are differences between forced copulations and reproductive copulations. These include a higher lifted tail, relaxing muscles and prone position to allow for a successful

intromission. During forced copulations females do not exhibit these strategies. Results of this study are consistent with previous literature suggesting the male and female waterfowl genitalia have coevolved due to sexual conflict by forced copulation. This study presents new findings of female responses to reproductive copulation by adjusting to alleviate the counter morphology of the male. This study is relevant to my topic as it provides this new evidence of reproductive copulation, as well as an example to the resistive morphologies the females have evolved through natural selection.

Evidence of phenotypic plasticity in penis morphology and delayed reproductive maturation in response to male competition in waterfowl

Brennan, Patricia L. R., Ian Gereg, Michele Goodman, Derek Feng, and Richard O. Prum. "Evidence of Phenotypic Plasticity of Penis Morphology and Delayed Reproductive Maturation in Response to Male Competition in Waterfowl." *The Auk* 134, no. 4 (2017): 882–93.

<https://doi.org/10.1642/AUK-17-114.1>.

Phenotypic plasticity is an important trait to organisms within changing environments, as it presents the ability to express different traits in response to these changes. Little is known about the relation between phenotypic plasticity and sexual competition. In this study, Ruddy ducks and Lesser Scaup were used as test species. The Lesser Scaup (*Aythya affinis*) forms mating bonds seasonally, have forced copulations with extra males, and are known to have shorter penises. Ruddy Ducks (*Oxyura jamaicensis*) are promiscuous, reproductively aggressive, have long penises, and few males are known to copulate with females. Male-male competition was hypothesized to be greater in Ruddy Ducks and therefore are hypothesized to have larger ratios

of phenotypic plasticity in response. Males from each species were grouped based on population density, where the influencing factor would be whether males would be paired or not due to limited female numbers. Penis lengths were measured during the breeding season over two consecutive years. Average lengths were higher in the Lesser Scaup when under high-competition social environments. Ruddy Ducks, however, did not show any significant difference in penis size between social groups. Instead, they showed delayed reproductive maturation affected by body size and social environment. In male-dominated environments, Lesser Scaup phallus length increased regardless of age and body size. Ruddy Ducks showed increases in body size as their penis sizes are already long in comparison to their body size. Ruddy Ducks were found to grow longer phalluses before the breeding season, suggesting that the competition between males either delays overall maturation while increasing sexual maturation, or limits ability to maintain a matured penis throughout the breeding season. A limitation to this study is the fact that female subjects could not be studied without sacrificing the female, therefore an accurate representation of plasticity within these duck populations may only be attributed to male anatomy. This study supports my research as it provides more insight to the evolutionary theories surrounding the development of sexual competition in the waterfowl species.

Forced copulation results in few extrapair fertilizations in Ross's and lesser snow geese

Dunn, Peter O., Alan D. Afton, Mark L. Gloutney, and Ray T. Alisauskas. "Forced Copulation Results in Few Extrapair Fertilizations in Ross's and Lesser Snow Geese." *Animal Behaviour* 57, no. 5 (1999): 1071–81. <https://doi.org/10.1006/anbe.1998.1066>.

Extrapair paternity (EPP), mating with individuals other than mating partners, may occur in up to 70% of offspring in some species of birds but little is known about the factors influencing EPPs. In this study, extrapair paternity was observed in Lesser Snow Geese and Ross's Geese, which contain some of the highest frequencies of extra pair copulations globally. Mating pairs were observed for three years with blood samples collected for determining parental analysis in the last year of the study. Analysis show that extrapair paternity is related to the frequency of extrapair copulations. EPPs were found in less than 5% of young in both Snow Geese and Ross's Geese, even though approximately half of the attempted copulations were by extrapair males. All extrapair copulations observed were forced, suggesting this is not a successful breeding tactic. This supports other literature hypotheses that suggest females may use their coevolved anatomy to select against fertilizations by forced copulation. Some error may include the fact there were some dumped eggs into other nests, which may have effects on the resulting analysis. This paper is relevant to my study as it describes the low probability of success of forced copulations, supporting the fact that female reproductive morphologies can be selective against these types of copulations.