A Quacktical Guide to Coevolution: Phallus Scales as a Sperm Competition Strategy in Waterfowl

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BIOL 4141: Evolution

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November 23, 2025

Abstract:

Coevolution between waterfowl sexes can be described as an 'evolutionary arms race' between sexes as both males and females have developed genitalia that counter each other's effect. Females possess counter-spiralled vaginas and dead-ended pockets, whereas males produce spiralled penises with scaly morphology. Recent experimental studies are limited and have not yet understood why these traits occur in waterfowl species. I aim to identify the purpose of scaly phallus morphology under the sperm-competition hypothesis by which waterfowl are hypothesized to remove sperm of other mating males from the female's vagina. This study will add to the ever-growing evidence supporting the coevolution of genitalia while providing a mechanism of evolution at play in waterfowl species.

Introduction:

Natural selection constitutes three objectives to be considered at play: variation of the trait among a population, increasing fitness of the individual if the trait is acquired, and heritability of the trait. While most birds possess simple genitalia, waterfowl are one of the few extant bird orders that still retain the male intromittent organ (Briskie and Montgomerie, 1997). These species seem to have coevolved elaborate genitalia morphologies and complexities such as spiral shaped penises in males and counter-spiralled vaginas in females (Brennan et. al, 2007). Females also present longitudinal dead-ended sacs, which are hypothesized to prevent sperm from travelling to the ovum (Brennan, et. al, 2007). These morphologies have been proven present among three phylogenetic lineages of waterfowl: Oxyura (stiff-tailed ducks), Anas (dabbling ducks), and Clangula (diving ducks) (Brennan et. al, 2007). In a study by Brennan et al., this phylogenetic analysis suggests there is variation in waterfowl penis length among waterfowl species, proving there is a mechanism of natural selection at play in this lineage (Brennan et. al, 2007).

Previous hypotheses have supported the evolutionary origin of the male intromittent organ in waterfowl by way of coevolution with forced copulations, female preference, and male confidence (Briskie and Montgomerie, 1997). In studies comparing simple genitalia/sexual copulation species to complex genitalia/forced copulation species, evidence suggests the evolution of complex female genitalia has coevolved antagonistic characteristics to counteract reproduction through forced copulation (Brennan, et. al, 2007). A study by Dunn, et al. shows that this coevolution of genitalia may occur to counteract the forced copulations seen within these lineages where Lesser Snow Geese and Ross's Geese presented offspring with less than 5% of young exhibiting extra-pair paternity from forced copulations (Dunn, et al., 1999). These studies provide evidence of heritability and selection for coevolution in waterfowl by working against the complex morphology traits seen in males. While variation is shown regarding waterfowl copulatory traits, the strategies that increase individual fitness are still unknown.

Though evidence to suggest the coevolution of genitalia complexity is present, there have been no in-depth studies into the sperm-competition theory (Coker, et al. 2002). This theory states that natural selection of males should favour those who increase reproductive success, specifically through increasing sperm count and testes size (Møller & Briskie, 1995). Research by Møller & Briskie found testes mass is positively related to extra-pair paternity and sperm production, proving to be another strategy to male competition (1995). By using extra-pair paternity copulation strategies, males can maximize fitness through siring multiple broods of offspring (Møller & Briskie, 1995). Therefore, by spreading his genes at higher rates throughout the population, a male can maximize his reproductive success through sperm competition.

Sperm removal strategies provide competition for paternity and are seen within many animal lineages, specifically in insects, dunnock birds, and marine species (Davies, 1983; Kamimura, 2000; Wada et al., 2005). In insects, some species use their phallus to remove sperm from other males, namely Tenebrionid beetles, damselflies, and dragonflies (Kamimura, 2000). Cuttlefish use their arms III to remove sperm masses from female mates (Wada et al., 2005). Additionally, in other avian species like dunnocks, cloacal pecking extrudes the sperm of another male through pecking at the female's cloaca (Davies, 1983). These species are hypothesized to have evolved these strategies in systems where females likely endure multiple matings by other males (Kamimura, 2000).

Due to the presence of scaly morphology on the male waterfowl's intromittent organ, it is hypothesized that males may have evolved these complex morphologies not only for grip while performing internal fertilizations, but also to compete with other males by removing sperm from the vagina, as seen in insect species (Coker, et al. 2002). This hypothesis supports the sperm-competition theory as sperm displacement adds a variable to remove competing sperm, maximizing the reproduction attempt by a new male with a female. Waterfowl phallus scales point toward the base of the penis, suggesting that they use a scraping motion during withdrawal of the organ, the mechanism of which has not been studied (Coker, et al. 2002). The sperm-competition theory would prove evolutionarily useful as intraspecies and male-male competition pressures should prompt more selection for removal strategies in addition to features like phallus length.

Methods and Experimental Design:

To address the gaps in the evolution of the male phallus in waterfowl species, I propose a study on the basis of the sperm-competition theory, specifically in measuring whether scaly phallus morphology can be used as a sperm removal strategy. The study will take place in the late spring between May and June. This study will be conducted in Quesnel, B.C., an overlapping breeding ground for Lesser Scaups, Ruddy Ducks, and Mallard Ducks, whom are all species of three clades of waterfowl exhibiting a copulatory organ (Burger, 2015a, 2015b; Davidson, 2015). The Bufflehead duck will act as a control species of which has simple genitalia morphology, does not exhibit forced copulations, and who's breeding grounds also occur in the Quesnel area (Brennan et al., 2007; Robertson & Goudie, 2020). Breeding pairs may be found in areas of the Quesnel Hydraulic Road, Soda Creek Road, Nature Education & Resource Centre located downtown Quesnel, and in Ten Mile Lake Provincial Park (Wildlife Viewing in the Cariboo Region, n.d.).

To obtain data on individuals, I will band waterfowl to provide unique identifying codes per individual waterfowl, then, conduct a genetic analysis on each bird to further determine individuality. Breeding pairs will be noted and banded similarly for pair identification. Feather samples will be collected from each individual under CCAC guidelines and will be sent to a lab for further DNA fingerprinting. Additional individual measurements such as mass, wing length, and breeding pairs will be recorded upon feather collection and banding.

Once breeding pairs are identified, nesting locations will be set up with trail cameras to identify when copulations occur. Because avian species possess the ability to retain sperm internally, this study can be conducted within two weeks of initial insemination (Sasanami, et al., 2013). Cameras will be checked manually every two days to determine whether breeding has occurred. Once a breeding event has occurred, I will travel to the breeding pair to capture the male and collect swabs of his penis to determine the presence/absence of another male's DNA. Swabs will be taken around the base, middle, and tip of the phallus, concentrating effort under the scales, as well as the vagina of the breeding female. These swabs will also be sent to the lab to determine DNA traces, of which I can compare to my own database. Copulations will be separated based on whether they occurred with a mated or extra-pair male. Bufflehead ducks will be used as a control to determine where the presence or absence of sperm can be detected in simpler genitalia without other inseminating males. Results will be analyzed through statistical software such as R Studio (version 4.4.3) and JASP (version 0.95.4), specifically by ANOVA and independent t-test where applicable, the aim of which is to identify whether birds with complex, scaly morphology are more likely to remove sperm of other males in comparison to birds with simple genitalia, and where these removing areas on the phallus are located.

Significance:

This study will identify gaps in research regarding fitness qualities of waterfowl, aiding the understanding surrounding evolutionary mechanisms in birds retaining a copulatory organ. Because the coevolution mechanism of waterfowl genitalia is unknown, understanding morphology evolution is important to determine why female waterfowl are retaining genitalia that reject male advances. If scaly morphology is not used to remove a competing male's sperm, other mechanisms may reject the current coevolutionary hypothesis, further complicating our understanding on the origin of these spiral anomalies. Few studies dare to address the twists and turns that are waterfowl genitalia, and this study aims to help quack the case.

Conclusion:

Recently published experimental studies on the coevolution of waterfowl genitalia are extremely limited, most citing studies that occurred over 20 years ago. This study is important to continue the understanding of genitalia coevolution in waterfowl and to answer why some bird species not only retain an intromittent sex organ, but who also compete in what is described as an 'evolutionary arms race' for control of copulation (Leisler & Winkler, 2020). Future studies may address the amount of sperm retained on the phallus, or if sperm may be saved in the female's vagina for delayed insemination by utilizing the dead-ended pockets within the female anatomy.

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