

Quick guide Bird genitalia

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Wait, do birds have genitalia? Most birds — 97% of all species — do not have external genitalia, and copulate via a ‘cloacal kiss’ where the cloaca of the male and female briefly touch while the female takes up the sperm. Male phalluses are found in about 3% of all avian species, and they can be fully intromittent — long enough to penetrate the female vagina — or non-intromittent — an enlargement of the cloaca that does not enter the vagina. The male phallus has been retained from the ancestral form shared in all amniotes, and is found only in the most basal avian species including the Paleognathes, such as the Ostrich, Emu, Rhea and Tinamou (Figure 1), as well as a few Neognathes, specifically in the Galloanseriformes that include ducks and fowl. At the split of Neoaves — the ‘modern’ birds — the external male genitalia were lost. The female phallus that in most amniotes becomes the clitoris is present early in development, but has yet to be described in any adult bird. The vagina is the first segment of the female reproductive tract, in between the cloacal entrance and the shell gland, and it is typically a folded tube covered with connective tissue. This segment is present in all birds, regardless of whether males have a penis or not.

Why did birds lose their penises?

The evolutionary loss of the penis remains an evolutionary mystery. Why lose an appendage designed to deliver sperm close to female eggs in species with internal fertilization? Scientists have proposed that losing the penis may lighten up body weight for migration, but ducks are among some of the longest distance migrants, and have very large penises. Losing the penis could shorten copulation duration to prevent predation, but existing data do not support this idea. Two hypotheses that may turn out to explain penis loss in birds are that losing the penis may help to minimize transmission



Figure 1. The intromittent penis of a Great Tinamou (*Tinamus major*).

Tinamous and other Paleognathes have spiraled intromittent penises, visible here immediately after mating, whereas many Galliformes have non-intromittent penises that are not externally visible. (Photo: Raul Fournier.)

of sexually transmitted diseases, or that penis loss may have evolved as a response to female choice for less violent males.

If some birds have penises, how come we never see them?

The penis in most birds is kept inside out in a pocket in the cloaca, and it inflates with lymph rather than blood. Lymphatic erection makes it difficult for males to keep their penis stiff for long periods of time, since lymph is a low-pressure system, so the penis is never erect prior to copulation, rather it unfolds inside the female, so there is no way to see it until copulation is over. The exception seems to be ostriches, which have a solid collagenous shaft with little erectile spaces that is not inverted inside the cloaca, but simply brought back inside. This lymph-powered penis is an evolutionary novelty in amniotes, where most penises are inflated by blood.

How variable are bird genitalia?

Ostriches and kiwis have asymmetric penises that bend to the left, but all other birds appear to have coiled phalluses of varying length. All of them

have external sperm channels that coil around the outside of the penis, and they are all powered by lymph. There are many species differences in the length and girth of the phallus, and the elaboration of its surface that can sometimes have ridges, bumps or even keratinized spines. Vaginas are equally variable, with changes in their length, width, and elaboration that can range from a simple folded tube in most birds to a virtual labyrinth filled with blind end pouches and spirals in some waterfowl.

What explains variation in genitalia?

Both penises and vaginas grow seasonally. Penis seasonality is related to levels of testosterone and dihydrotestosterone, with the penis growing during the late winter and early spring, and shrinking in late summer. While the entire female reproductive tract undergoes size reduction just like the penis, reduction in vaginal size has not been studied. Waterfowl are the only avian group where genital variation has been studied in the context of their mating system, in particular sexual conflict. Scientists have found that the size and elaboration of the penis

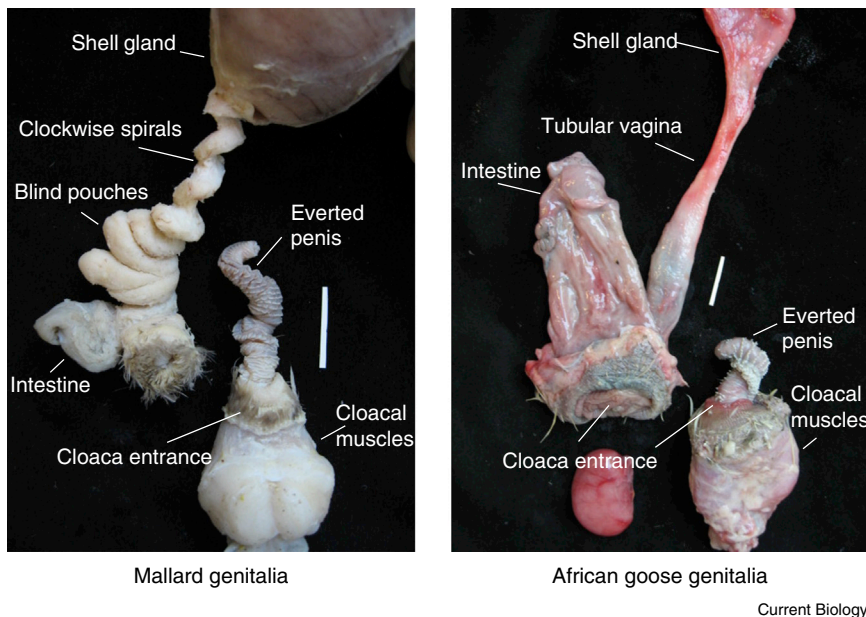


Figure 2. Genital coevolution in waterfowl.

Male and female genitalia coevolve in waterfowl. When levels of forced copulations are high and penises are long like in the mallard (*Anas platyrhynchos*), the female vagina is convoluted and complex (left panel), whereas when forced copulation is absent and penises are short like in this African goose (*Anser cygnoides*), the vagina is a straight tube (right panel). Scale bar = 2 cm. (Photo: Patricia Brennan.)

correlates with the degree of forced extra-pair copulations that bachelor males can impose on females who are already paired with a mate for the season (Figure 2).

How do you know waterfowl vaginas really evolved to make insemination by unwanted males more difficult? Fertilization success of forced copulations is very low, so even when such copulations are common (30–40% of all observed copulations), most of the offspring are still sired by the female's own mate, not by the force-copulating males (96–97% paternity). In addition, experiments with artificial vaginas shaped like the female vagina show that eversion of the penis is stopped in convoluted vaginas, forcing the males to ejaculate further from the areas of sperm storage and fertilization.

How does the penis get lost or reduced in birds? The mechanism of phallus development is evolutionarily conserved in birds and mammals, and within birds it is the same in birds with (e.g. ducks) and without (e.g. chicken) an intromittent penis.

The phallus grows from two genital swellings that develop between the cloacal lips, and merge to form a single structure with a sperm channel in the middle. In the chicken, the phallic body undergoes cell death at the tip of the growing organ, whereas in ducks no cell death occurs and a large intromittent penis can grow. The female phallus becomes the adult clitoris in other vertebrates but, as mentioned, no clitoris has been described in adult birds. However, in female birds, a phallus is seen early in development. In ducks, female phallus development is similar to that of the phallus of male and female chickens, which raises the possibility that male phallus reduction utilized the pre-existing pathway of female phallus formation. If this is indeed the mechanism, this would help explain why the phallus has been lost or reduced multiple times in birds.

What are some interesting avenues for future research? Male–male competition affects penis morphology in some waterfowl: the penis in the Lesser Scaup (*Aythya affinis*) grows longer and earlier in the season when males are kept in competitive groups,

compared to males housed alone with a female. However, male Ruddy ducks (*Oxyura jamaicensis*) housed in groups become reproductively suppressed by a dominant male who is the only one that grows a large penis for the entire length of the breeding season, whereas males housed alone with a female can always grow a long penis. This socially mediated genital plasticity is not well understood and the morphological response may vary in other species depending on their mating systems. The effect of social environment on vaginal morphology remains unknown, but vaginas will likely respond to changes in the risk of forced extra-pair copulations, and this would be an interesting avenue of further research. A larger comparative study would help us understand how ecological and behavioral factors might influence genital morphology in birds at large, a question that may help us understand why male genitalia were lost in most birds.

Where can I find out more?

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