

AVIAN GENITALIA

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SCIENTIFIC THOUGHT often is intimately associated with the attitudes and cultures in which scientists are immersed. I experienced an example of this a few years ago, when Bob Montgomerie and I were searching the literature for information on the intromittent organs of birds. Our plan was to write a review of the subject and to examine the question of why most birds lacked something that seemed so fundamental to reproduction (Briskie and Montgomerie 1997). It soon became clear that the material we required was incomplete and fragmentary. For example, it was well known that male waterfowl (family Anatidae) possessed an intromittent organ, but we could find no information on the closely related screamers (family Anhimidae). Eventually, we dug up an anatomical description of one screamer species from the last century. The work was marvelously detailed and beautifully illustrated, with all of the features of the plumage, skeleton, muscles, and digestive organs presented. But when it came to the genitalia, the relevant regions of the figures and descriptions were mysteriously blank! Victorian sensibilities apparently prevented a discussion of such unmentionables, even among the scientific establishment. It took a trip to a private aviary in England to examine the cloaca of a live bird before we could settle the matter (yes, screamers have a penis).

Such prudishness may seem comical today, but it is only in the last few years that evolutionary biologists have taken more than a passing interest in the genitalia of birds. This renewed interest stems from a general upsurge in studies of sexual selection and a desire to understand how this process has shaped the evolution of birds. Beginning with an examination of variation in testis size among shorebirds (Cartar 1985), comparative studies on sperm morphology, ejaculate size, sperm storage, and cloacal protuberance anatomy soon followed (Møller 1988, Birkhead and Hunter 1990, Briskie and Montgomerie 1992, Birkhead et al.

1993). These early studies quickly revealed two things. The first was that much of the interspecific variation in size or elaboration of avian reproductive organs seemed to be a product of sperm competition: species with high levels of sperm competition tended to have larger testes and cloacal protuberances and to produce longer sperm and bigger ejaculates than less-promiscuous species. The second revelation was just how much we had underestimated the diversity of avian genitalia.

Genital anatomy has never featured as prominently in avian taxonomy as it has in invertebrate or mammalian research (King 1981). Perhaps because of this lack of attention, our knowledge of the diversity of structure and function of avian reproductive organs lags behind that of other groups. However, a spate of recent papers is quickly correcting this situation. For example, Wilkinson and Birkhead (1995) studied the phalloid organ of the Greater Vasa Parrot (*Coracopsis vasa*) of Madagascar and discovered that this structure is fully intromittent. A preliminary examination of its structure indicated it is not homologous with the intromittent organs in other birds and so must have evolved independently. In the Superb Fairy-Wren (*Malurus cyaneus*) of Australia, the cloacal protuberance of males carries an odd cartilaginous tip (Mulder and Cockburn 1993); its function is a mystery. Cloacal protuberances are also found in other passerines, but the size of this structure can reach gigantic proportions in some species (e.g. Smith's Longspur [*Calcarius pictus*]; Briskie 1993). In Alpine Accentors (*Prunella collaris*), not only do males have a huge protuberance, but the lips of the female cloaca also swell and become the centerpiece of elaborate precopulatory displays (Nakamura 1990). Additional studies suggest that we have only scratched the surface, and that much remains to be discovered about the reproductive anatomy of birds.

A study of the Bearded Tit (*Panurus biarmicus*) by Sax and Hoi (1998) in this issue of *The Auk* takes the study of avian genitalia beyond simple description. By examining the devel-

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opment of the cloacal protuberance at the level of the individual, they provide some intriguing evidence that investment in genitalia depends very much on the social circumstances of each male. In most species of passerines, the cloacal protuberance of males is formed by an expansion of the seminal glomera (distal ends of ductus deferens) outside the body cavity (Wolfson 1954). The protuberance acts as a storage organ for sperm and has long been used by banders as a method for determining the sex of birds (e.g. Pyle et al. 1987). However, in the Bearded Tit, the protuberance consists mostly of a gelatinous mass covered by a muscle layer. The seminal glomera are positioned more medially than in any other passerine and contribute only minimally to the structure of the protuberance. And, unlike in other species, the protuberance everts during copulation, revealing a large, red phallus-like structure that probably functions as a copulatory organ (Birkhead and Hoi 1994). The high level of extrapair paternity in Bearded Tits (ca. 30% of nests contain extrapair young; Hoi and Hoi-Leitner 1997) suggests that the unusual structure of their cloacal protuberance is associated with intense sperm competition (Birkhead and Hoi 1994).

The testes of birds have long been known to increase in size prior to breeding and then regress after laying. Sax and Hoi (1998) found a similar pattern in the size of the cloacal protuberance of Bearded Tits. Protuberance size first increased over the spring, peaking at about the time females laid their first egg. It then declined steadily until the initiation of second broods, at which point the decline was rapidly reversed. Bearded Tits produced up to three broods per season, and for each subsequent breeding attempt, the protuberance increased and decreased in conjunction with the fertility cycle of the female. The dramatic decrease in protuberance size (and testis size) immediately after laying and its regressed state throughout the nonbreeding season indicate that such structures are costly to maintain. What these costs might be have not yet been identified, although presumably they include the extra energy required for maintenance and flight, and disease. That the cost of genitalia can be high is suggested by the rapidity with which the protuberances shrink after breeding: protuberances had already diminished to half

their maximum size by the time nestling Bearded Tits hatched (Sax and Hoi 1998).

If high costs favor a rapid regression of male genitalia after breeding, then a low benefit may prevent development in the first place. Sax and Hoi (1998) found that unmated male Bearded Tits had significantly smaller cloacal protuberances than mated males. Unmated males also had smaller testes and far less sperm in their seminal glomera than mated males. There was no correlation between protuberance size and any characteristic of males that could be related to female choice (e.g. size, plumage ornaments) and, hence, mating status. This suggests that it was the social circumstances of the male, and not his quality, that triggered the development of genitalia. Indeed, experimentally isolated males failed to show any signs of protuberance development, even during the breeding season. Only when exposed to females did virgin males develop fully functional cloacal protuberances. Thus, male Bearded Tits appear unwilling to invest in the costly production of a large protuberance if the opportunity for copulations is limited.

The lack of genital development by unmated and virgin male Bearded Tits contradicts the current view from sperm-competition theory that all males should try to maximize their reproductive success through extrapair copulations (Birkhead and Møller 1992). If males are unlikely to sire offspring unless paired with a female, then there may be little benefit in developing reproductive organs until paired. The fact that unmated males had undeveloped or poorly developed gonads during the breeding season suggests that these males are excluded from breeding and so would face a considerable disadvantage in the pursuit of copulations. In Bearded Tits, at least, the development of genitalia appears to be facultative and subject to the mating opportunities perceived by each male.

It took ornithologists a century to fully appreciate the importance of sexual selection in the evolution of avian behavior. Although we are still in the early stages of documenting diversity in the structure of avian reproductive organs, the findings of Sax and Hoi (1998) suggest that the strategies employed by different individuals in the development of their reproductive tissues will be as complex as that seen in their behavior. Sorting out the proximate

mechanisms and the adaptive significance of such strategies no doubt will provide much to occupy researchers over the next decade. Perhaps 100 years from now, our century will be judged as overly obsessed by sex, but then, we too are the product of our time.

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