Sexual selection and the intromittent organ of birds

James V. Briskie and Robert Montgomerie


Unlike most animals with internal fertilisation, few extant bird species have a male intromittent organ (IO). Although two previously published hypotheses have attempted to account for the rare presence of IOs in birds, phylogenetic evidence suggests that it is the absence of an IO in the majority of bird species that requires explanation. Previous hypotheses suggested that IOs help minimise water damage to sperm when copulation occurs on the water (Water Damage Prevention Hypothesis) or that IOs help the sexes stay in genital contact when males have difficulty balancing during copulation (Maintaining Genital Contact Hypothesis). We find some limited support for these two ideas but there are so many exceptions that neither is particularly compelling. Because IOs are found in several flightless birds, it has also been suggested that IOs were lost to decrease the costs of flight (Minimising Flight Costs Hypothesis), however the cost of transporting an IO is expected to be minimal. We suggest, instead, that IOs may have been lost to minimise the risk of contracting pathogens and parasites during intromission (Avoidance of Sexually Transmitted Disease Hypothesis). Unlike most other homeotherms, birds have a cloaca that is common to both the urogenital and gastrointestinal systems, which may make birds more susceptible to sexually transmitted diseases. Unfortunately, the lack of comparative information on sexually transmitted pathogens in birds prevents a convincing analysis of this idea. We also present two new hypotheses based on the costs and benefits of IOs as a result of sexual selection. On the one hand, IOs may be favoured when paternal investment is high – an IO can increase a male’s confidence of paternity by ensuring that sperm are deposited well up into the female’s reproductive tract (Sperm Competition Hypothesis). This idea is supported by an association between IOs and male parental care during incubation. Alternatively, we suggest that male IOs may have largely disappeared in birds because of female preference for males without IOs (Female Choice Hypothesis), thereby allowing females more control over fertilisation. We argue that such a mechanism is plausible when females can afford to abandon eggs fertilised by males with IOs. This hypothesis is supported by the fact that species without IOs generally have relatively smaller, and presumably less costly, eggs than species with an IO. Preliminary data from other tetrapod vertebrates are also largely consistent with the Female Choice Hypothesis. Although the small number of independent evolutionary losses of IOs in birds precludes rigorous statistical tests of these hypotheses, the recent discovery of secondary modifications in male genitilia that function as IOs may help us understand the conditions under which the avian IO has been retained or lost over evolutionary time.

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The male intromittent organ (penis, hemipenis, false penis, etc.; hereafter IO) found in many animal species is clearly associated with internal fertilisation (e.g. Eberhard 1985). When fertilisation is external, some kind of male organ for the transfer of sperm to the ova seems unnecessary and potentially detrimental due to injury, disease or developmental costs. Indeed, we know of no animal species with external fertilisation that...
Table 1. Taxonomic distribution of intromittent organs (IOs): + and − indicate presence or absence, respectively) and modes of fertilisation in the tetrapod vertebrates.

<table>
<thead>
<tr>
<th>Class</th>
<th>Order</th>
<th>No. of species</th>
<th>IO</th>
<th>Fertilization</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphibia*</td>
<td>Gymnophiona</td>
<td>150</td>
<td>+</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>Caecilia</td>
<td>310</td>
<td>−</td>
<td>mainly internal</td>
</tr>
<tr>
<td></td>
<td>Mammalia</td>
<td>3</td>
<td>−</td>
<td>unknown</td>
</tr>
<tr>
<td></td>
<td>Salientia</td>
<td>2510</td>
<td>−/+</td>
<td>mainly external</td>
</tr>
<tr>
<td>Reptilia*</td>
<td>Testudines</td>
<td>250</td>
<td>+</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>Rhynchocephalia</td>
<td>1</td>
<td>−</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>Squamata</td>
<td>5820</td>
<td>+</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>Crocodylia</td>
<td>21</td>
<td>+</td>
<td>internal</td>
</tr>
<tr>
<td>Aves*</td>
<td>Struthioniformes</td>
<td>10</td>
<td>+</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>Tinamiformes</td>
<td>46</td>
<td>+</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>Craciformes</td>
<td>55</td>
<td>+/−</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>Austeriformes</td>
<td>147</td>
<td>+</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>Psittaciformes</td>
<td>358</td>
<td>+/−</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>Passeriformes</td>
<td>5700</td>
<td>+</td>
<td>internal</td>
</tr>
<tr>
<td>Mammalia*</td>
<td>All other orders</td>
<td>2440</td>
<td>−</td>
<td>internal</td>
</tr>
<tr>
<td></td>
<td>All orders</td>
<td>3500</td>
<td>+</td>
<td>internal</td>
</tr>
</tbody>
</table>

* Data from Goin et al. (1978).
† Number of species from Howard and Moore (1991); IO and mode of fertilisation from King (1981).
‡ Males do not have an IO in the Megapodidae (personal observation; centre Campbell and Luck 1985).
§ Males have an IO in two species Coracopsis (Wilkinson and Birkhead 1995); IOs are absent in all other Psittaciformes.
¶ Males have an IO in the two species Bulbulornis (Sushkin 1972); IOs are absent in all other Passeriformes.
# Data from Eckstein and Zuckerman (1956).

possess an external sperm transfer organ. It seems likely, then, that IOs serve an adaptive function in the internal transfer of sperm from male to female during copulation.

Birds, however, are enigmatic in this context—fertilisation is always internal yet in only a small proportion (about 3%) of species there is any kind of IO. In bird species with an IO, the male organ is usually inserted briefly into the female's vagina before sperm is transferred, while copulation in all other birds involves only cloacal contact (called the "cloacal kiss" by ornithologists) during which sperm is transferred to the female. Because IOs are rare in birds, most attention has focused on explaining their presence (e.g. Lake 1981, King 1981) but it is real absence from the majority of bird species that is most interesting—birds are the only vertebrate class in which internal fertilisation without an IO is the predominant mode of insemination (see Table 1).

In this work, we review and evaluate two hypotheses previously proposed to explain why only a few bird species have IOs. We then present four new hypotheses (one based on flight costs, one based on the risk of pathogen transmission and two based on the role of sexual selection) to explain why IOs are largely absent from birds. Other treatments on the evolutionary significance of IOs in animals have focused on the elaboration of male genitalia (e.g. Eberhard 1985, Brownell and Ralls 1986, Dixon 1987, Harcourt and Gardiner 1994) or on the general patterns associated with internal fertilisation (Greenwood 1975). Eberhard (1985) invoked sexual selection to explain the diversity of elaborate IOs within a taxon, but our hypotheses suggest that sexual selection might also explain the pattern of presence/absence of IOs in animals in general.

The avian phallus

Despite a common function in transferring spermatozoa to the female, the avian phallus can take a variety of forms (Fig. 1). To help orient the reader we begin with a brief description of the avian phallus, derived from a comprehensive review of its anatomical structure (King 1981) and from recent work on its elaboration in different bird species (e.g. Birkhead et al. 1993a, Briskie 1993, Mulder and Cockburn 1993, Birkhead and Hoi 1994, Wilkinson and Birkhead 1995).

Intromittent organs

The avian phallus can be classified into two functional types: true intromittent organs (IOs), which are inserted into the female's cloaca during coition, and non-intromittent organs, which do not enter the cloaca but instead deposit sperm directly onto the external genitalia of the female.

The most common type of IO is formed by an outpocketing of the ventral wall of the cloaca (Fig. 1a, b). In its detumescent state this type of IO lies entirely within the male's cloacal cavity and only during erection is it everted through the vent and visible externally. The mechanism of erection is thought to be lymphatic and not blood-vascular as in most reptiles and mammals (King 1981). During ejaculation, semen passes
along a recessed sulcus on the outside surface of the organ and not through an enclosed internal tube as in mammals. IOs formed by outpocketings of the cloaca can be further divided into two forms, depending on the presence or absence of a blind tubular cavity within the phallus. An IO with no such cavity occurs in the families Apterygidae (kiwi), Tinamidae (tinamous) and Struthionidae (ostrich). This is thought to be the most primitive or ancestral form of the avian phallus and most closely resembles the IOs of turtles (order Testudinata) and crocodiles (order Crocodylia). In birds, IOs with a cavity are found in all species in the following taxa: the families Rheidae (rheas) and Casuariidae (cassowaries and emus), the order Anseriformes (waterfowl), and possibly the family Cracidae (curassows, guans and chachalacas). Thus within the Struthioniformes all species in the families Rheidae and Casuariidae have IOs with a cavity, whereas all species in the families Struthionidae and Apterygidae have IOs without a blind cavity, suggesting that this trait may have evolved more than once within a lineage. Variation in the size of the IO from one species to the next (King 1981, personal observations) further supports the idea that the morphology of this structure may be a relatively plastic trait.

IOs are also present in the Vasa parrots (Coracopsis spp., family Psitacidae) of Madagascar (Fig. 1c; Wilkinson and Birkhead 1995) and the buffalo weavers (Bubalornis spp., family Ploceidae; Fig. 1d) of Africa. In both genera, the phallus is intromittent, yet they differ anatomically from each other and from the IOs found in the Boaves. In the Vasa parrots, a large "cloacal protrusion" is formed by the eversion of the cloaca. This protrusion is inserted into the expanded cloaca of the female during copulation bouts that may extend over an hour (compared to copulations lasting no more than several seconds in most bird species, even those with IOs). The structure of the cloacal protrusion has not been studied in detail so it is not known if this organ is homologous to the other IOs described above. This protrusion is, however, highly vascularised and thus may be eroded by engorgement with blood rather than by the lymphatic system used in other birds with IOs. In contrast, the phallic organ of buffalo weavers is a stiff, rod-like structure, permanently outside the body cavity, just anterior to the opening of the vent (Fig. 1d; Sushkin 1927, Bentz 1983, Birkhead et al. 1993a). This IO is mostly bare, non-creepie connective tissue, containing no ducts, and therefore cannot itself directly transfer sperm to the female. Phallic organs are found in both sexes, although they are much enlarged in males. The exact role the phallic organ plays in copulation is not clear, although it is thought to have an intromittent function (Birkhead et al. 1993a).

Non-intromittent phallic

A non-intromittent phallus also occurs in some birds, particularly in the order Galliformes (guinea fowl, grouse and quail; Fig. 1e) and possibly some songbirds (order Passeriformes). Non-intromittent phalli share many structural similarities with IOs except that they are short and cannot enter the female reproductive tract. Instead, the two lymphatic folds of the inner cloaca evert during copulation to form a median furrow, which collects the semen and places it in a position where it can be readily taken up by the female during cloacal apposition. In passerine birds, this process is assisted by the eversion of two conical papillae from the wall of the male’s proctodeum (Wolffson 1954); in some species (e.g. Parnicus biarmicus, Birkhead and Hoi 1994), the everted male cloaca is quite striking and forms a large, red phallus, terminating in a small

Fig. 1. Diversity in structure of the avian phallus. All redrawn from original drawings and photos in the publications listed, but not to scale since no scale was provided on the originals. Unless noted, all drawings are right lateral views with the bird's head toward the top right of the page. (a) Ventral view of the erect intromittent organ (IO) of the Greater Rheas Rhea americana (after King 1981). (b) Erect IO of a duck Anas sp. (after King 1981). (c) Erect intromittent organ of the Greater Vasa Parrot Coracopsis vasa (after Wilkinson and Birkhead 1995). (d) Phallic organ of the Buffalo Weaver Bubalornis alboventris (after Bentz 1983). (e) Erect non-intromittent phallus of the Domenic Turkey Meleagris gallopavo protruding from the spread lips of the vent (after King 1981); bird's head is toward top left. (f) Clasped protrusion of the Superb Fairy-wren Malurus cyaneus showing carunculous tip in front of vent (after Mulder and Cockburn 1993). Legend (terminology mainly from King 1981): c.o.f. = caruncular fold, f. = feathers, m.u. = muscles, p.b. = phallic bodies, p.o. = phallic organ, s.p.h. = sulcus of phallus, v. = opening of vent, v.i. = lips of vent.
papilla. It is not known if this papilla is intromittent in this or any other species; however, because of their small size, it is likely that most papillae function merely to place ejaculates onto the surface of the female’s external genitalia. The non-intromittent phallus of galliforms and passerines generally resembles the crocodilian and testudine phalli in structure, but it is not as well developed. This anatomical homology suggests that the intromittent capability has been lost during evolution by a reduction of the ancestral phallus (King 1981).

The region around the vent in most passerine males also becomes greatly enlarged during the breeding season by the development and extrusion of the seminal glomera (the terminal ends of the ductus deferens) to form a cloacal protubrance (Fig. 1f). The cloacal protubrance is not known to be inserted into the female in any species. However, Wolfson (1954) suggested that one function of the protubrance may be to act as a copulatory organ and assist in coition – by elevating the vent of the cloaca from the body wall, better contact with the cloaca of the female would be possible. In some species, the protubrance is enormous (e.g. Pruella collaris, Nakamura 1990; Calcarius pictus, Briskie 1993) but this large size seems to be associated mostly with increased sperm storage in the seminal glomera and does not enhance copulation efficiency or speed (Birkhead et al. 1993b, Briskie 1993). The cloacal protubrance of the Bearded Tit Panurus biarmicus similarly becomes greatly enlarged, but unlike other species, the bulk of the protubrance is filled with gelatinous connective tissue and not the seminal glomera (Birkhead and Hoi 1994). In the Superb Fairy-wren Malurus cyaneus, the anterior surface of the protubrance has become further modified into a cartilaginous tip that is not erectile (Fig. 1f; Mulder and Cockburn 1993). It is not currently known what role, if any, this cartilaginous tip plays in copulation.

Phylogeny

Because IOs are present mainly in relatively “primitive” birds, it has been suggested that their absence in most species might possibly be explained by phylogenetic inertia (King 1981). This would not, of course, provide a functional explanation for the loss of an IO during avian evolution but it would indicate that its absence in most species might be explained as a phylogenetic constraint after its initial loss. In such a situation, patterns that might provide a functional explanation for the loss of an IO could be obscured even in the face of considerable variation in potential causal factors.

To recreate the phylogenetic history of IOs in birds, we have relied on a recent phylogeny of living species based on DNA-DNA hybridisation (Sibley and Ahlquist 1990). While this phylogeny is not universally accepted (see Mayr 1989), it seems to be based on consistent, objective criteria and is the most complete avian phylogeny currently available. Moreover, this phylogeny provides at least as conservative a view of the evolutionary history of IOs (i.e. minimum number of losses or gains) as any other recent bird phylogeny (e.g. Storer 1971). Throughout this paper we also use the Sibley and Ahlquist (1990) classification for living birds down to the level of tribe, and Howard and Moore (1991) for genera and species names. For the classification and phylogeny of other vertebrate taxa, we used McFarland et al. (1985) and Goin et al. (1978).

The Sibley and Ahlquist (1990) phylogeny for birds suggests that almost all living species (class Aves) can be readily divided into two large infraclasses, Eoaves (469 species in 5 orders) and Neoaves (about 8500 species in 17 orders). All 246 species having true IOs are in the infraclasse Eoaves (Fig. 1), except the Vasa parrots (2 species; family Psittacidae) and the buffalo weavers (2 species; family Passeriformes), which are in the Neoaves. Thus, IOs occur in almost half of the species of Eoaves but in less than 0.1% of the Neoaves; IOs occur in 26.1% (6/23) of all avian orders and 8.3% (12/142) of all families (Table 1).

From the phylogeny of living birds (Fig. 2), it can be seen that the IO is an ancestral character in the Eoaves, since it is also present in the Crocodylia, the extant sister taxon of Aves (Gauthier 1986, Hedges 1994). Moreover, birds are thought to have evolved from dinosaurs and there is some evidence from the structure of caudal vertebrae that dinosaurs possessed IOs (Larson 1994). An IO is also present in the embryos of male pigeons Columba livia but is resorbed before hatching and is thus absent in the adult (Hasimoto 1931). This suggests that the ancestors of pigeons (and perhaps all the other modern birds lacking IOs) possessed an IO that has been subsequently lost. We assume, then, that IOs were present in the earliest birds, but have been lost from most clades over evolutionary time.

From the phylogeny of living birds, we suggest that IOs have been lost at least three times in the class Aves – in the family Megapodidae, in the order Galliformes, and in the infraclasse Neoaves (Fig. 2). Alternatively, the IO may have been lost in the evolutionary lineages leading to the infraclasse Neoaves and the superorder Gallomorphae (composed of the Craciformes and Galliformes) and later regained in the family Cracidae. IOs also appear to have been regained at least twice in the Neoaves – once in the Vasa parrots (genus Coracopsis), and once in the buffalo weavers (genus Bufulornis). As the anatomical structure of the IO in both of these genera differs fundamentally from that found in the Eoaves, it appears that IOs have evolved de novo in these groups and have not been retained from the ancestral lineage. Either way, at least five evolutionary events are required to explain the pattern of presence/
absence of IOs in birds. The presence or absence of IOs is also conserved within most avian orders and families (see Fig. 2) suggesting that some phylogenetic constraint may operate at the family level or higher.

Whichever evolutionary scenario is correct, it is clear that avian IOs were not simply lost or regained once in evolutionary time. This does not, of course, discount the possibility that the general absence of IOs in the lineage leading to the Neoaves, or within families or orders of the Eoaves, is due to some phylogenetic constraint after their initial loss. It does, however, allow us to look for common characteristics that might explain the functional significance of the independent losses and gains of these organs in each lineage.

Hypotheses

Previous speculation on the adaptive significance of IOs in birds (e.g. Lake 1981, King 1981) has resulted in two published hypotheses about why some birds have IOs.

In this section, we review these two hypotheses and then present four new hypotheses that view the problem using a phylogenetic perspective, asking why only a few groups have retained an IO while IOs have been lost from the majority of avian lineages over evolutionary time. IOs should be retained when fitness benefits exceed costs in males and should disappear from a lineage when fitness costs exceed benefits. We outline the logic for all six hypotheses below and, using data compiled from the literature, we assess the potential of each hypothesis to explain the general pattern of occurrence of IOs in birds. We also discuss the ability of these hypotheses to explain the patterns of IO presence/absence in other vertebrate classes.

Since avian IOs have been lost only three times and regained only twice in the evolutionary history of this vertebrate class (Fig. 2), it is not possible to apply rigorous statistical methods to evaluate the six hypotheses that we present. Normally, we would apply statistical methods that control for phylogeny (e.g. Harvey and Pagel 1991) to this problem, but with only five
Table 2. Distribution of intraspecific organs (IOs) and copulation sites in aquatic birds.

<table>
<thead>
<tr>
<th>IO</th>
<th>Family</th>
<th>Species*</th>
<th>Typical site of copulation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Land</td>
</tr>
<tr>
<td>Present</td>
<td>Anatidae</td>
<td>132 (135)</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Dendrocygnidae</td>
<td>6 (8)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Rallidae</td>
<td>12 (122)</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Laridae</td>
<td>79 (119)</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td>Scolopacidae</td>
<td>3 (83)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Podicipedidae</td>
<td>20</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Phalaronidae</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Sulidae</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Athingidae</td>
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<td>2</td>
</tr>
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<td></td>
<td>Phalacrocoracidae</td>
<td>32</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Pelecanidae</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Sphenicidae</td>
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<td>9</td>
</tr>
<tr>
<td></td>
<td>Gaviidae</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Procellariidae</td>
<td>99</td>
<td>10</td>
</tr>
</tbody>
</table>

* number of aquatic species (total number of species in family is shown in brackets).

independent evolutionary events such an analysis lacks statistical power. Instead, we simply present the evidence for and against each hypothesis without any statistical analyses or controls for phylogeny. With detailed information on variation in IO size and structure within clades, it should be possible to evaluate these hypotheses more rigorously in the future. We, therefore, present these hypotheses as a stimulus for further study rather than as a comprehensive analysis designed to test the various alternatives.

Natural selection hypotheses

Hypothesis 1: Water damage prevention

For birds that copulate on the water, an IO may be advantageous because it prevents water from entering or washing out the female’s cloaca during copulation, either damaging spermatozoa or diluting the ejaculate (Lake 1981). Both osmotic shock and dilution are likely to have negative consequences on fertility so any mechanisms that ensure that water does not come into contact with sperm should be favoured. Thus, by acting both as a plug and as a device to place sperm further up in the female’s urogenital tract, an IO could provide an adaptive advantage in species that copulate on water by helping to minimise water damage.

If an IO provides an advantage for copulation on water, then a clear pattern is predicted among aquatic birds – species without an IO should come ashore to copulate, while those with an IO should copulate on the water. To evaluate this prediction, we compiled information on the copulation sites of aquatic species (Table 2). We defined aquatic species as those that regularly sit on the water during their breeding season. For example, three species of “waterfowl” in the family Anatidae (Coscoroba coscoroba, Branta sandvicensis, Chloephaga picta) were not considered aquatic because they rarely enter the water during the breeding season (Johnsgard 1978). In most cases we used only secondary sources (e.g., Cramp and Simmons 1977–1983, Johnsgard 1965, 1978) for data. For each species we scored the site where copulations have been observed – copulation site is not known for some species and these were tabulated as unknown (Table 2).

The expected pattern among aquatic birds is found both at the family and species levels (see Table 2). Both families of aquatic birds having IOs typically copulate on the water whereas 11 of the 12 families of aquatic birds lacking IOs typically copulate on land. In 3 families (Anatidae, Laridae and Pelecanidae), there are a few exceptions that deserve further consideration but the overwhelming majority of aquatic species fit the expected pattern. Among aquatic species for which we have data, 84 of 88 (95.5%) with IOs copulate on the water whereas only 10 of 106 (9.4%) species without IOs do so.

The prevalence of land-based copulations in the majority of aquatic bird species lacking an IO (Table 2) supports this Water Damage Prevention hypothesis and argues that such birds would be at a disadvantage if they copulated on the water. However, several species of aquatic birds without IOs apparently copulate successfully on water (puffins, auks, mergansers, pelicans and phalaropes), suggesting that an IO may not always be necessary to minimize water damage during copulation. Moreover, among the 246 species with an IO only 84 (all within the Order Anseriformes) are aquatic species known to typically copulate on the water whereas 112 (from 12 families within 7 orders) are terrestrial species that copulate on land (copulation sites for the remaining 49 species are not known for
certain). Thus the presence of IOs in a wide variety of species from 12 families cannot be explained as a general adaption to minimise water damage.

For the Anatidae, Anseranatidae and Dendrocygnidae that copulate on land, the presence of an IO could be explained as a phylogenetic constraint resulting from their recent evolution from more aquatic species. However, none of the remaining families having IOs are likely to have had a recent aquatic ancestor. Since the Water Damage Prevention hypothesis can only explain why it may be advantageous for aquatic birds to retain an IO, it cannot account for the loss of IOs in almost every other lineage of birds.

**Hypothesis 2: Maintaining genital contact**

An IO might also be advantageous whenever coition is difficult and/or inefficient because of physical complications imposed by the bird's anatomy or environment (King 1981). For example, about half of the avian families (but only about 5% of species) that have an IO are relatively large-bodied, long-legged, flightless birds (i.e. ostrich, rheas, cassowaries, and emus) that have largely lost the balancing capacity of their wings. Thus, cloacal apposition for these birds may present a physical challenge and, by acting as a guide or lock, an IO could ensure that semen is properly positioned to enter the female reproductive tract during copulation. As discussed above, waterfowl (order Anseriformes) may also experience this difficulty because they typically copulate on water, an unstable substrate.

We evaluated this Maintaining Genital Contact hypothesis by determining whether long-leggedness in birds is related to the possession of an IO. Birds with relatively long legs may experience greater difficulty in positioning themselves during copulation because their centre of gravity is high and therefore they would be more likely to benefit from the greater stability provided by an IO. We categorised all families of birds as either “long-legged” or “short-legged” according to their height relative to body length (excluding the tail, neck and head). Birds with legs greater than 50% of their body length were classified as long-legged and birds less than this as short-legged. Measures of body length and height were taken from a variety of field guides and handbooks (e.g. Cramp and Simmons 1977–1983, Fry et al. 1988).

While these categorisations are clearly arbitrary, they do allow us to make a crude quantitative assessment of this hypothesis. Using these criteria we identified 25 families containing at least one long-legged species but only 5 of these families (20%) possess an IO. Short-legged birds were characteristic of 117 families of which 7 families (6.0%) contain at least one species that possesses an IO. Although these data suggest that IOs are somewhat more common in families with long-leggedness, the absence of an IO in so many long-legged birds and its occurrence in 7 families (within 5 orders) of short-legged birds suggests that maintaining contact during coition is unlikely to be the primary reason for presence of IOs in birds. In fact, it is unclear whether an IO can provide much additional advantage in helping males maintain genital contact during coition. Instead, males balance during copulation primarily by (1) grasping the female's neck, bill or head with their bill, (2) holding the female's wings, back or sides with their feet, and/or (3) flapping their wings rapidly (e.g. see Cramp and Simmons 1977–1983). In our search of the literature we found descriptions for one or more of these behaviours in at least one species in all 23 orders of birds and almost every family. This suggests that even with an IO, birds must employ other behavioural methods to ensure proper positioning and balance during copulation. Indeed, when Ostriches Struthio camelus and Emus Dromaius novaehollandiae copulate, the female crouches on the ground (Cramp and Simmons 1977–1983, Marchant and Higgins 1990) even though the male has an IO. Thus it is unlikely that an IO has been retained as an adaption to ensure successful coition in those birds in which large size has made balancing difficult.

**Hypothesis 3: Minimising flight costs**

Since four of the families with IOs (Struthionidae, Raphidae, Casuariidae, Apterygidae) are completely flightless and 2 of the remaining 6 families with IOs fly either weakly or only when forced (Tinamidae, Cracidae), it might be expected that IOs were lost as an adaptation to lessen the costs of flight. This hypothesis has been suggested to us by several ornithologists but we are unable to find reference to it in the literature. Only in the four families of Anseriformes and the buffalo weavers (Bubulornis) are there IOs in strong, agile fliers. Moreover, in support of this hypothesis, IOs reach their most prodigious size in the 4 flightless families.

This hypothesis, however, is weak for several reasons. First, even the largest avian IO must weigh less than a small meal and is thus unlikely to make an important contribution to the cost of flight. Second, in those families in the Neoaves that have lost the IO (Phasianidae, Numididae, Odontophoridae, Megapodiidae), males travel about mainly on foot, flying only when flushed or when moving relatively long distances (Johnsgard 1988). In contrast, the four families of waterfowl (all with IOs) are generally strong fliers, with some species undertaking annual long-distance migrations. Third, there has been no reappearance of the IO in any of the >60 flightless species in the Neoaves. Finally, IOs are found in all bats (Micro- and Megachiroptera; Eckstein and Zuckerman 1956) and apparently do not hamper their ability to fly. Thus there seems to be no compelling reason why an IO would add significantly to the costs of flight.
Hypothesis 4: Avoidance of sexually transmitted diseases
Unlike the vagina in most mammals, the avian cloaca serves as a common passage for both the urogenital and the gastrointestinal systems. During copulation, the male's IO must enter the female's cloaca, thus exposing both sexes to a potentially more hostile environment of pathogens and parasites than in organisms where the two openings are separate. We argue that the cloaca is a potentially hostile environment for genitalia because it comes into direct contact with faeces and, unlike the cloaca of reptiles, it is continuously warm in birds.

Although little is known about the transmission and virulence of most sexually transmitted diseases (STDs) in wild birds, some STDs can be a serious source of mortality in domestic fowl (see review in Sheldon 1993). For example, goose venereal disease can cause up to 10% mortality and reduce body mass, fertility and egg production in infected birds (Stipkovic et al. 1986, Marius-Jestin et al. 1987). Thus selection may favour the reduction and eventual loss of an IO as a way of reducing the probability of disease transmission. In species without an IO, copulation typically involves only brief (often less than 1.0 s) contact of the external lips of the cloaca, and this is unlikely to be as favourable for the transmission of pathogens as intromission involving extensive contact between the male IO and the female cloaca and vagina.

Although the Sexually Transmitted Disease hypothesis assumes that the risk of STDs is greater in birds than in other animals, there are currently no data available to test this idea. Nonetheless, avoiding STDs is unlikely to be a general explanation for the loss of the IO in all birds since it cannot explain why the IO is still present in some groups. Perhaps birds with IOs obtain other benefits through intromission that outweigh any potential cost of STDs (see sexual selection hypotheses below). The Sexually Transmitted Disease hypothesis also cannot explain the presence of an IO in the monotreme mammals (platypus and echidnas) which are homeotherms that similarly have a cloaca common to both the urogenital and gastrointestinal systems. Clearly, STDs have the potential to increase the cost of an IO, but whether or not this cost is great enough to lead to the evolutionary loss of the IO in most avian lineages remains unknown.

Sexual selection hypotheses
Since an IO is unnecessary (in birds) for the transfer of sperm to the female, this male organ may function as a secondary sexual character and thus may be influenced by sexual selection. One obvious advantage of an IO is that it can ensure both that sperm enters the female reproductive tract and that sperm is placed as close as possible to the site of fertilisation. In birds without an IO, the vagina must be everted into the cloaca during copulation to receive semen from the male (Lake 1981). Conceivably, a female could prevent or reduce the chances of subsequent fertilisation by refusing to evert her vagina or by ejecting sperm from the cloaca (Davies 1983). Lake (1981), for example, found that semen artificially placed into the cloaca of domestic fowl resulted in only 25.8% fertility of eggs laid in the subsequent 2–8 days, whereas fertility increased to 93% when semen was placed directly into the everted vagina. Since fertility can depend upon whether the vagina is everted, females may be able to retain considerable control over fertilisations (even after forced copulations) when the male does not have an IO. In contrast, males with an IO may be more successful in placing semen directly into the vagina without the cooperation of the female, thereby giving the male greater control over both copulation and fertilisation. These factors suggest the following two new hypotheses that might explain the existence of IOs in birds.

Hypothesis 5: Sperm competition
Male control of fertilisation is likely to be most important in those species in which females mate with more than one male during a breeding episode and males invest heavily in offspring. Because selection acts against males that invest in offspring that are not their kin, any mechanism that decreases cuckoldry will be favoured (Trivers 1972). We suggest that an IO increases the likelihood of paternity by providing males with more control of copulation and thereby ensuring that semen is placed directly into the female reproductive tract, or that ejaculates from other males are displaced.

Since any structure that increases the confidence of paternity for a male should be favoured by selection, all male birds should have an IO unless the costs (e.g. STDs) exceed the benefits. Thus the benefits of an IO are most likely to exceed its costs when a male provides a large amount of parental care relative to that provided by its mate. Alternatively, when female investment is larger than that of the male, selection should favour females that discriminate among males (Trivers 1972). Since retaining control of copulation and fertilisation is one way of discriminating between high and low quality males, female preference may be the mechanism that prevents the retention of IOs when male investment is low (see Hypothesis 6 below). Under this scenario, the control of fertilisations is seen as an arms race between the sexes (see Dawkins and Krebs 1979) and the sex that invests most in offspring care is likely to be the most discriminating.

To determine whether high levels of male investment are correlated with the presence of an IO in birds, we compiled data on the division of labour between the sexes during incubation. We used incubation behaviour instead of parental feeding because the latter is not easily comparable between altricial and precocial spe-
cies. Data were available for 96 of the 142 families of birds. In most families the overwhelming majority of species for which we could obtain data had the same relative male-female roles so these families were categorized by the prevalent pattern alone. Ten of the 96 families, however, were scored in more than one category because more than one mode of parental incubation was represented by a substantial proportion of species.

As expected, in those families with an IO, males invest heavily or exclusively in incubation while female-biased or female-only incubation prevails in families without IOs (Fig. 3). Although these results generally support our hypothesis that IOs have been lost in lineages with relatively higher levels of female investment, there are several exceptions to the predicted pattern. For example, among the avian families with IOs, both the Anatidae and Cracidae have female-only incubation. In birds without IOs, male-biased care is found in several species of Scopophiidae and is typical in the Jacanidae, Rostratulidae, Turnicidae and Pchelonematidae. These groups clearly do not support our hypothesis, but it is possible these exceptions represent cases of a recent acquisition of female or male-biased incubation patterns for whatever reason where development or loss of an IO has not occurred because of some phylogenetic constraint.

It is also possible that sperm competition may play a role in the evolution or retention of an IO independent of parental care patterns. For example, many of the ratites and tinamous have polyandrous or polygynandrous mating systems, in which the intensity of sperm competition is expected to be high (Birkhead and Møller 1992). Both Vasa parrots and bufalo weavers, two groups in the Nectarini in which an IO has reappeared, have much larger testes than expected for their body size (Birkhead et al. 1993a, Wilkinson and Birkhead 1995). As testes size in birds increases with the intensity of sperm competition (Møller and Briskie 1995), this suggests that these species too may have secondarily evolved an IO as an adaptation to intense sperm competition. Brownell and Ralls (1986) have argued that sperm competition has led to increased penis size in baleen whales, although the mechanism that would make this size increase advantageous is not clear. Perhaps, as in some insects (e.g. damselflies), the avian IO could be used to directly remove or displace sperm from rival males (Wagne 1979). Whether the avian IO functions in such a manner is currently unknown: the elaborate cork-screw pattern of ribbing on the external surface of some IOs (Fig. 1a, b) suggests that some sort of sperm removal or displacement is possible.

**Hypothesis 6: Female choice**

Female choice might also influence the patterns of occurrence of IOs in birds, if females can reduce the costs of IOs to themselves (e.g., by reducing STDs) while increasing the costs of IOs to males. Eberhard (1985) has also argued that the elaboration of male penises, particularly in insects, may be due to female choice, though by a different mechanism than we suggest here (see below). Our hypothesis is derived from the observation that when males do not have an IO, females have the potential to refuse sperm transfer from a male, or upon allowing a male to inseminate, to then expel or eliminate the ejaculate (Davies 1983). We suggest that such female behaviour will be possible and favoured only when females are able to abort fertilised ova at relatively low cost. Because bird ova are fertilised one at a time and usually 24 h or more apart, birds have the potential to abort single fertilised ova simply by laying eggs in places where they will not be incubated or by discarding them from their nest. To the best of our knowledge, this potential is unique among vertebrates that have clutch size > 1 – in other taxa ova are fertilised in batches and thus the abortion of single zygotes is potentially more problematic.

We suggest that females can afford to resist male copulation attempts or eliminate ejaculates only when they can afford to waste eggs. If the ancestral situation is such that males have an IO, female preference for males without IOs can evolve whenever females can afford to be choosy by disposing of ova fertilised by
we obtained data on 272 of the 469 species of Eoaves, including at least one species in each family. We did not include data from the Megapodiidae in this analysis because they have a unique method of incubation (in mounds of soil or rotting vegetation), unusually large eggs, and exceptionally precocial young (no parental care after hatching). As predicted, species in which males have IOs have larger eggs relative to female body mass than those without IOs (Fig. 4).

This comparative analysis thus provides some initial support for the Female Choice hypothesis. If this hypothesis is correct, we predict that forced copulations should be most common in species with IOs. The large number of reports of forced copulation in waterfowl (McKinney et al. 1983, 1984) would seem to support this prediction.

**Other vertebrate classes**

We can now ask whether our sexual selection hypotheses are generally applicable to other vertebrate taxa—they should also be applicable in invertebrates but there are too few species in which the male does not possess some kind of IO (see Eberhard 1983). If our sexual selection hypotheses are correct, IOs should be found in taxa with internal fertilization that also have either relatively high pro-laying maternal investment (as predicted by the Female Choice hypothesis) or considerable post-laying male investment in the raising of offspring (as predicted by the Sperm Competition hypothesis). We restrict our discussion here to the tetrapod vertebrates because the pattern of occurrence of IOs in the bony fishes, in particular, suggests that this trait is quite variable both among and within families (e.g., Meyer and Lydeard 1993). Thus an assessment of the pattern of occurrence of IOs in fishes will require a more detailed analysis and may be used as an independent test of the sexual selection hypotheses presented here.

In mammals, male IOs are universal (Eckstein and Zuckerman 1956). In this class female investment in offspring is considerable, usually involving long periods of internal gestation of embryos and obligate provisioning of milk for often long periods of growth and development after the young are born (Eckstein and Zuckerman 1956). Thus the pattern in mammals supports the Female Choice hypothesis but is contrary to the Sperm Competition hypothesis since most male mammals invest little in parental care (Kleiman and Malcolm 1981). There is evidence, of course, that female mammals can abort unwanted embryos (Hayssen 1984, Huck 1984) but this may be relatively costly physiologically, compared to simply leaving unwanted embryos in places where they will not develop, as birds can do.
In reptiles (snakes, lizards, turtles and crocodylians), oviparous species have high pre-laying investment by females, much like that provided by female mammals before parturition (Shine 1980). All reptile species have internal fertilisation (Table 1) and all have IOs except the tuatara (Order Rhynchocephalia). In oviparous and ovoviviparous species, considerable parental care is provided only by female crocodylians and some squamates. Although little care is provided by either sex in the remaining species, eggs are laid (and presumably fertilised) in batches and may undergo some development within the female before they are laid (Shine 1985). Thus we argue that female reptiles have high investment and little opportunity to dispose of single eggs fertilised by unwanted males. These patterns are all consistent with the Female Choice hypothesis but in the virtual absence of reptilian species without IOs, it is not possible to reject alternative hypotheses.

In amphibians (class Amphibia), there is diversity in both the site of fertilisation and in the presence of an IO. In caecilians (order Gymnophiona) fertilisation is internal and all species have an IO (Table 1). As with reptiles, eggs are fertilised in batches and either laid as a group or retained in the oviduct until hatching. Thus there would appear to be little opportunity for females to abandon embryos fertilised by a single male at low cost. Thus data from caecilians are consistent with the Female Choice hypothesis. In salamanders and newts (order Caudata), fertilisation is external in the suborder Cryptobranchidae (hellbenders and Asian land salamanders) and internal in the Salamandridae (salamanders and newts) but IOs are not present in either of these taxa. In the Salamandridae the transfer of gametes is indirect in most species, involving no physical contact between the sexes. Instead, males produce spermatophores that are taken up indirectly (e.g. from the ground or other substrate) by females and stored in a spermatheca. In all species, females thus have the opportunity to reject unwanted spermatophores. As a result, fertilisation is operationally external in most species and the evolution of an IO would not be expected.

In most species of frogs and toads (order Anura), fertilisation is external (Table 1). A few species in the families Bufonidae and Leptodactylidae, however, have internal fertilisation and copulate by cloacal apposition. In all of these species, fertilised eggs develop within the female and thereby constitute considerable maternal investment. The absence of an IO in these species is a clear exception to the predictions of the Female Choice hypothesis and deserves further study.

The only amphibian so far discovered with an IO is the North American frog *Asephus truit* in which males develop a spiky penis just before the late summer-to-autumn mating season (Metter 1964a). In this species the females lay relatively large eggs which she keeps (apparently fertilised) inside her until the following summer (approximately 6 months after fertilisation) when they are released into the streams in which these animals live (Metter 1964b). It has previously been suggested that the IO of *Asephus* is an adaptation to copulation in the cold, fast-flowing streams inhabited by this species (Goin et al. 1978). Our Female Choice hypothesis, however, provides an alternative explanation and allows us also to account for the lack of IOs in other frogs which mate in cold water and/or streams. On balance, then, the available information from the amphibians is largely consistent with the Female Choice hypothesis but more data on pre-laying maternal investment and the relative contribution of males to offspring care are needed for a critical test.

**Conclusions**

We conclude from the data presented here that the two previous hypotheses proposed to explain the distribution of IOs in birds (Water Damage Prevention, Maintaining Genital Contact) are not particularly convincing as general explanations. We did, however, find some support for two new hypotheses based on sexual selection theory. As is often the case (see Bradbury and Andersson 1987), it may be difficult to separate the influence of the two aspects of sexual selection (male-male competition and female choice) — both agents of selection may be applicable and reinforcing in this case. Indeed, it is possible that the presence/absence pattern of IOs in birds can best be explained by more than one hypothesis (Hilborn and Stearns 1982). For example, though we discounted the Water Damage Prevention and Maintaining Genital Contact hypotheses as useful general explanations for the retention of IOs, both of these mechanisms could favour the retention of IOs in certain situations. Our analyses necessarily addressed only one hypothesis at a time. In the absence of experimental studies, we can only await more data on the correlates of intra- and interspecific variation in IO size and structure to help to unravel the complexities of multiple causation.

One useful way of looking at the adaptive significance of IOs in birds is to examine the fitness costs and benefits to both males and females — IOs should be selected against and disappear from a lineage when costs exceed benefits. Clearly, both males and females will benefit from male IOs under the Water Damage Prevention and Maintaining Genital Contact hypotheses, simply by making copulation more efficient and more likely to result in fertilisation. On the other hand, the Avoidance of Sexually Transmitted Disease hypothesis suggests a cost to both males and females when males have IOs, at least in birds. The two sexual selection hypotheses suggest a benefit of IOs only to males either by enhancing paternity (Sperm Competi-
tion hypothesis), or by allowing them to place sperm far enough into the female reproductive tract that it cannot easily be eliminated by the female after copulation (Female Choice Hypothesis). Thus, if sexual selection has had an influence on the presence/absence of IOs in birds, it has probably resulted in sexual conflict between males and females over paternity.

Eberhard (1985) also suggested that sexual selection via female choice was the most likely hypothesis to explain the elaboration of male genitalia in a wide variety of animals. He suggested that male genitalia function as a form of internal courtship – males with more elaborate structures are preferred by females because they provide an index of male quality, or simply through runaway processes (see Pomiankowski 1988 for the distinction). Our sexual selection hypotheses differ dramatically from Eberhard's in that we suggest that female birds prefer males without IOs. We do not see that our hypotheses are incompatible with Eberhard's because they are really about different things – presence/absence of IOs vs elaboration of IOs given that they are present. The wide range in relative size of IOs in birds (even within families like the Anatidae, personal observations) suggests that Eberhard's (1985) hypothesis may apply within taxa that have IOs.

Though the patterns that we have described in other vertebrate taxa will be interesting to look at more closely, our analysis especially suggests several avenues for further study in birds. First, we clearly need to know more about the patterns of occurrence of IOs in this class. Our survey of the literature showed that knowledge of the presence of IOs in birds is far from complete and it would be useful to have more detailed descriptions of these organs. Possibly because IOs have not figured prominently in avian taxonomy, such descriptions are rare. Recent observations of a variety of secondary modifications of the avian phallus confirm that there is still much to be learned about the diversity and function of IOs even in some of the most common and well-studied birds (e.g. Birkhead et al. 1993a, Birkhead and Hoi 1994, Briskie 1993, Mulder and Cockburn 1993, Wilkinson and Birkhead 1995). With more detailed descriptions it should also be possible to assess the influence of mating systems on the relative sizes of IOs to test more critically our Sperm Competition Hypothesis. Similar detailed descriptions of the IOs and reproductive biology of buffalo weavers and Vasa parrots would permit a further independent test of our sexual selection hypotheses.

Second, our Sperm Competition Hypothesis assumes that males with IOs can place sperm further into female vagina than can males without such organs. Some detailed study is needed on the relative placement of sperm by males with and without IOs to make a critical test of this assumption. Since such analysis is generally not possible in closely related species (except Vasa parrots and buffalo weavers compared to other members of their families), we suggest that it might be most profitably done comparing species similar in size with similar copulation behaviour (like ducks and penguins). Moreover, in some insects (e.g. damselflies, Waage 1979), the penis functions not only in inseminating females but also in removing ejaculates from rival males. A similar role for the avian IO remains entirely speculative at this point, but if found, such a function would further support our hypothesis that IOs in birds evolved as an adaptation to sperm competition.

Finally, we need to know more about the reactions of females to both forced and unforced copulations by male birds in species with and without IOs. Our Female Choice Hypothesis assumes that females can avoid copulation, and possibly even avoid using inseminated sperm, if the male does not have an IO. While there are other ways that a male may force insemination (e.g. by threatening injury), our hypothesis still requires the likelihood of fertilisation to be higher when the male has an IO. Presumably males without IOs sometimes force copulations (see McKinney et al. 1984) because there is a chance of successful insemination (review in Birkhead 1988, Birkhead and Moeller 1992), but we need to know if those forced inseminations can later be eliminated by the female. If these assumptions prove correct, then it is possible that IOs have evolved primarily as a result of the selective advantages accruing to males that force copulations. That such control may conflict with female interests is suggested by the rarity of IOs among bird species in which females have the ability to lay and abort eggs singly and at relatively low cost. By holding eggs “hostage” to the male, most female birds may have succeeded in controlling inseminations, effectively selecting for the loss of the male IO.

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