

## Review

# Sexual conflict in waterfowl: why do females resist extrapair copulations?

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Forced copulation is a male reproductive strategy in a variety of animals but rare among avian species, with the notable exceptions of waterfowl (family Anatidae) and at least 1 passerine species, the New Zealand stitchbird or hihi *Notiomystis cincta*. The presence of forced extrapair copulation in these species challenges the perception that females control extrapair copulations (EPC) across avian species. A noteworthy behavioral discrepancy is believed to exist between waterfowl and passerines in that female waterfowl are widely assumed to always resist EPC, whereas female passerines often pursue EPC. This difference in female behavior between avian groups is perplexing in light of the fact that unconditional resistance to EPC exposes female waterfowl to risk of serious injury. I consider 5 hypotheses to explain the female unconditional resistance strategy in waterfowl and focus on the controversial idea that resistance could represent a female mate choice strategy in a system dominated by male force. This resistance as mate choice hypothesis relies on indirect benefits to females through biasing paternity in favor of manipulative or genetically high-quality males and predicts that unconditional resistance versus conditional acceptance of EPC reflects the presence or absence of forced copulation in the mating system. Although indirect selection is widely regarded as unimportant in the evolution of female defensive traits when direct costs are large, I argue that indirect selection could nonetheless play an important role in the evolution of female strategies under sexual conflict. *Key words:* birds, female resistance, forced extrapair copulation, indirect benefits, sexual conflict, waterfowl. [*Behav Ecol* 21:182–192 (2010)]

**F**orced copulation is a male reproductive strategy found in a variety of animal species, including some nonhuman primates and other mammals (Smuts BB and Smuts RW 1993), vertebrates (e.g., fish and frogs) (Bisazza et al. 2001), as well as invertebrates (e.g., insects) (Thornhill 1980). Forced copulation is rare among avian species, with the notable exception of waterfowl (family Anatidae), for which forced extrapair copulation (FEPC) has been reported in 55 species in 17 genera, accounting for about one-third of all species of waterfowl (McKinney and Evarts 1997). FEPC may be anatomically impossible among passerine species, in which males lack an intromittent organ (Briskie and Montgomerie 2001), but the New Zealand stitchbird or hihi *Notiomystis cincta* provides a conspicuous exception in its ability to overcome its anatomical constraints (Castro et al. 1996; Low 2005). Although extrapair copulations (EPC) are well documented among avian species, with extrapair offspring found in 90% of species studied (Griffith et al. 2002), the existence of FEPC in some species is intriguing in part because it presents an apparent counter-example to the pervasive view (e.g., Jennions and Petrie 2000) that females control and benefit from EPC in avian species (but see Arnqvist and Kirkpatrick 2005). This view has led researchers to frame studies of EPC in birds in the context of female fitness (for a review and assessment, see Westneat and Stewart 2003), but the existence of FEPC within a species suggests intersexual conflict,

and therefore the conflicting interests of both sexes must be taken into account in assessing the behaviors (Trivers 1972).

In this paper, I review empirical evidence on FEPC in waterfowl and consider several hypotheses for the existence of apparently unconditional resistance exhibited by female waterfowl. The idea that female waterfowl never accept EPC is well established in the literature (e.g., McKinney et al. 1983; Westneat and Stewart 2003), and much discussion and debate has centered on the evolution of this purportedly unconditional strategy (e.g., see Sorenson 1994b; McKinney and Evarts 1997; Cunningham 2003). Whether this behavior is truly as inflexible as suggested in the literature is a topic I will cover in a later section. However, given that female resistance to FEPC can expose females to high direct costs, the assertion that females never consent to some EPC to minimize costs presents a paradox. I explore major hypotheses on the evolution of this strategy and urge a reappraisal of the controversial idea that female waterfowl might use unconditional resistance as a strategy to reduce net costs through the indirect benefits gained by screening for genetically high-quality or manipulative males. This argument differs from the more extreme case for indirect benefits to females under ostensible sexual conflict (formulated most explicitly in Cordero and Eberhard 2003) in that it does not suggest that indirect benefits translate to net gains for females but rather that these benefits may simply offset some of the direct costs of forced copulation, which could help explain the otherwise perplexing behavior of unconditional resistance.

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### Waterfowl mating systems

Most species of waterfowl are socially (but not necessarily genetically) monogamous, with a generally low frequency of

social polygyny despite minimal paternal care (Oring and Saylor 1992). As polygyny is rare in most species, opportunities for males to increase breeding success tend to be limited to FEPC (Oring and Saylor 1992). Although the function of FEPC was once debated (for a history of ideas, see Burns et al. 1980), studies reporting that FEPC attempts peak in frequency during the egg laying period and tend to be directed at fertile females (e.g., Cheng et al. 1982; Sorenson 1994a, 1994b) strongly suggest that males pursue FEPC to inseminate more females. Female waterfowl are not known to solicit EPC and are generally reported to resist all EPC attempts by males, so all EPC is believed to be forced (McKinney and Evarts 1997). Forced pair copulations (FPC) are also reported in many species of duck (*Anas*), sometimes occurring after a male has witnessed his mate involved in FEPC (McKinney et al. 1983). This may serve to guard against cuckoldry by decreasing the likelihood that the sperm from the FEPC will fertilize the female's egg (Cheng et al. 1983).

### Forced copulation in waterfowl

The behaviors associated with forced copulation in waterfowl are reviewed thoroughly in McKinney and Evarts (1997). Briefly, FEPC is initiated by a male pursuing an extrapair female, then physically restraining her, mounting her, performing a tail bend and thrust (considered by some, but not all, authors to be evidence of intromission), and then dismounting. If the female manages to get away before intromission occurs, the male will usually chase the female, often for long distances in the air, on land, or underwater. Male–female chases may involve the female diving into water or hiding in vegetation and resisting vigorously if caught. FEPC may take place on land or in water and notably lacks the precopulatory and sometimes the postcopulatory displays of consensual pair copulations. FPC have been observed in several species (McKinney et al. 1983), and these FPC proceed similarly to FEPC but with less vigor on the part of both the male and the female. Females do not usually fly away or dive into water to escape FPC, and the male does not tend to be as persistent.

The presence of FEPC among species may be inhibited by ecological constraints, such as particularly harsh environments, which may force males of some species to devote the bulk of their time and energy to defending breeding territories (Oring and Saylor 1992). However, male strategies such as mate fidelity, paternal care, and full-time territory defense are favored by selection only in those habitats in which offspring survival depends heavily on biparental care (McKinney 1991).

### Direct costs to female waterfowl of resisting FEPC

FEPC can be costly to females both because mating itself can carry costs (as discussed in later sections) and because female resistance to EPC often involves a struggle with the male, which can expose the female to a high probability of injury or death. Importantly, costs of resisting FEPC are considered separately from costs of mating throughout this paper. In this section, the costs discussed are costs of resisting, that is, the increased likelihood of injury or death to females as a result of male–female struggles initiated by female resistance behavior. McKinney and Evarts (1997) and references therein report observations of females being injured or killed due to repeated FEPC attempts in mallards *Anas platyrhynchos*, northern pintails *Anas acuta*, white-cheeked pintails *Anas bahamensis bahamensis*, lay-san teal *Anas laysanensis*, and in several other dabbling ducks (*Anas* species). Female mallards have been found after FEPC attempts with few remaining feathers on the backs of their

heads due to grasping, deep scratches from being clawed, internal injuries including ruptured organs and eggs, and even occasional drowning (McKinney and Evarts 1997). Female resistance behaviors tend to be conspicuous and sometimes attract other extrapair males that join in on the chase (McKinney and Evarts 1997). Risk of injury or death may increase when multiple males pursue a female and sometimes take turns harassing or forcing copulation with her, as has been reported in blue-winged teal *Anas discors*, northern pintail, lesser snow geese *Chen caerulescens caerulescens*, as well as mallards, in which as many as 39 males have been observed chasing 1 female and in some cases multiple mallard males have been seen to mount a female in succession (McKinney et al. 1983 and references therein). The presence of multiple males chasing a single female does not imply that more than one—or indeed any—male will achieve copulation, but a struggle that involves multiple males suggests that the costs of resisting are probably higher.

It is unclear how high the risk of injury or death posed by resisting EPC is to the average female in any given species of waterfowl. Although reports of injury or death resulting from FEPC are often cited in the literature, these reports are almost always anecdotal and few studies have attempted to quantify the rate at which this behavior results in harm to the female. McKinney and Evarts (1997) cite 1 study by Huxley (1912) at the Tring reservoirs in England in which about 70 female mallards, an estimated 7–10% of the population, were killed annually due to FEPC. This is a high mortality rate that represents extreme costs to females, but McKinney and Evarts (1997) note that crowded or park populations of mallards tend to have an unusually high ratio of males to females, often subjecting females to continuous harassment. This may not be representative of most waterfowl populations, as discussed below, and other studies measuring rates of injury or death resulting from FEPC are needed.

### The intromittent organ in birds

Waterfowl are unusual in that they have an intromittent organ, which is found in only 3% of avian species (Briskie and Montgomerie 1997), including ratites (order Struthioniformes), tinamous (family Tinamidae), cracids (family Cracidae), screamers (family Anhimidae), the magpie goose *Anseranas semipalmata*, and waterfowl (King 1981). The intromittent organ of waterfowl is believed to facilitate their rare ability to force copulation with females (King 1981). Although the intromittent organ is absent in most avian species, it is believed to be the ancestral form, which has been lost in most clades (Briskie and Montgomerie 1997). New anatomical work paired with phylogenetic analysis suggests a complex history of male genitalic evolution in birds (Brennan et al. 2008), and it is likely that the observed patterns among species are best explained by more than 1 theory (Briskie and Montgomerie 1997). The intromittent organ may help prevent sperm damage in species that copulate on water (Lake 1981), facilitate genital contact in species with anatomical or environmental constraints (King 1981), and function in sperm competition to increase confidence in paternity in species with high paternal investment (Briskie and Montgomerie 1997; Coker et al. 2002; but see Brennan et al. 2008). The widespread loss of the intromittent organ in most avian species may reflect increasing efficiency of copulation (Wesolowski 1999), minimization of flight costs, avoidance of sexually transmitted diseases, or result from female choice in species in which females could afford to abandon eggs from forced copulations, reducing the advantage to males of maintaining an intromittent organ (for a review and evaluation, see Briskie and Montgomerie 1997, 2001).

### Waterfowl genital morphology

A recent study by Brennan et al. (2007) on the coevolution of female and male genital morphology in waterfowl found that females have complex vaginal morphology, including “dead-end” pouch cavities and 360° spirals that twist in the opposite direction of the male phallus. These findings could be interpreted either as evidence that female genitalia have evolved to minimize the direct costs of mating with males with intromittent organs, as discussed below, or, as Brennan et al. (2007) suggest, as adaptations that function to hinder insemination attempts without female cooperation. For example, the vaginal pouch cavities may prevent the phallus from fully everting, impeding sperm deposition further inside the cavity, while the spirals might serve as a barrier to entry (Brennan et al. 2007). An interspecific comparison found vaginal elaboration to be positively correlated with phallus length (Brennan et al. 2007), and phallus length and complexity have been shown across species to correlate with the frequency of FEPC (Coker et al. 2002). Together, these results suggest that female waterfowl may be engaged in an evolutionary arms race with males, whereby female morphological responses to prevent forced fertilization spur male morphology to promote it (Brennan et al. 2007). Brennan et al. (2007) conclude that female resistance, rather than sperm competition, is the primary selective force driving the evolution of male waterfowl genitalia, as sperm competition alone would probably not result in the observed coevolution.

An alternative hypothesis for the genitalic coevolution that was not considered by Brennan et al. (2007) is that the complex vaginal morphology of some waterfowl species has evolved to minimize damage by the male intromittent organ to the vaginal tract. An example of this sort of adaptation appears to occur in the true bug infraorder Cimicomorpha (Heteroptera), in which males possess hypodermic genitalia used to stab females in the abdomen, thereby completely bypassing the female genitalia (Stutt and Siva-Jothy 2001). Female bugs in turn have evolved special structures such as swollen, desclerotized sacs that may function to minimize damage (Morrow and Arnqvist 2003; Reinhardt et al. 2003; Tataric et al. 2006). Other examples of female morphological adaptations to reduce bodily harm during mating include the evolution of a more reinforced wall of the female bursa copulatrix in response to spinier male genitalia in seed beetles (Rönn et al. 2007), thickened “genital pads” in Malabar ricefish to reduce damage from the males’ sperm-filled darts, and a thickening of the dermal layer in areas where males tend to bite females during courtship in the Atlantic stingray (both reviewed in Arnqvist and Rowe 2005). However, examples of female morphological adaptations that appear to function to reduce damage, such as those mentioned above, tend to take the form of thickened skin or sac-like structures that probably absorb impact. More detailed inquiry into the functions of the waterfowl vaginal structures would be informative, as it is not presently obvious if or how the structures described by Brennan et al. (2007) would aid in reducing damage.

Another way in which female waterfowl morphology may function to reduce costs is by making it easier for females to thwart males in some manner similar to water striders *Gerris incognitus*, in which female structures appear to reduce the costs of male harassment by decreasing the time required to dislodge unwanted males (Arnqvist and Rowe 1995). However, the female structures in water striders are external spines that make it difficult for males to clasp females during mating struggles, whereas in waterfowl, the resistant morphology is internal, suggesting that it serves not to dislodge the male but rather to provide the female with some way of preventing

fertilization. However, the precise way in which female waterfowl morphology interacts with male morphology is not yet known, and it could be the case that elements of the female anatomy, such as the vaginal spirals, prevent males from initiating copulation. Follow-up studies that pair the new morphological data with behavioral observations will be necessary to elucidate the functions of such structures.

### FEPC in hihi

The hihi provides an unusual example of a passerine species with confirmed presence of FEPC, as well as a unique face-to-face mating posture believed to be used only during forced copulation (Castro et al. 1996). Hihi males tend to be either monogamous or polygynous, with both paired and unpaired males seeking EPC on other males’ territories during the breeding season (Low 2004). Castro et al. (2004) used DNA fingerprinting to determine paternity of hihi chicks in a nesting population and found that 46% of chicks resulted from EPC while 82% of broods had at least 1 extrapair young. Another study measuring extrapair paternity (Ewen et al. 1999) found that 35% of all chicks were extrapair, and about half of these were the offspring of unpaired males.

Unlike in waterfowl, 1 study found that female hihi occasionally consent to EPC, but only secondary females of polygynous males (Low 2005). Consensual copulation in hihi is similar to that in other avian species where the male mounts the female from behind while she stands (Low et al. 2005). However, FEPC in hihi is characterized by 1 or several males chasing a female and then 1 male forcing her onto her back, positioning himself on top of the female, and restraining the struggling female with his outstretched wings (Low et al. 2005). FEPC in hihi may be anatomically possible due to the sexually active male’s extremely large cloacal protuberance, which swells by almost 400% during the breeding season (Low et al. 2005). The cloacal protuberance is believed to function similarly to an intromittent organ, allowing males to force copulation with females (Low et al. 2005), by bypassing various methods of female resistance such as redirecting or obstructing the cloacal vent or ejecting sperm (Briskie and Montgomerie 2001). The unique face-to-face forced copulatory position of the hihi is also thought to aid males in achieving FEPC by allowing for longer duration of mating, which gives the male more time to discharge a large amount of semen into the female and less chance for her to eject it (Low et al. 2005).

### Female resistance and FEPC in passerines and other birds

Instances of apparent forced copulation and female resistance to EPC across bird species are reviewed in a number of publications (e.g., Westneat et al. 1990; Wagner 1991; Gowaty and Buschhaus 1998; Westneat and Stewart 2003). Although female and male behaviors vary substantially across species, authors note the consistent difficulty of distinguishing between female resistance to avoid EPC and its associated costs and female resistance as a ploy to incite competition among males (Westneat et al. 1990; Westneat and Stewart 2003). In addition, EPC that appears to be forced has sometimes been shown to be under female control as in the purple martin *Progne subis*, a passerine species, in which females have been reported to subtly accept EPC from older males (Wagner et al. 1996). Female razorbills *Alca torda*, a species of auk, have been shown to control EPC by only allowing males to inseminate them when they had the potential to benefit, even though many extrapair interactions appear to be aggressive (Wagner 1991).

In passerines, FEPC attempts have been reported in many species but may be anatomically impossible (McKinney and Evarts 1997). Such attempts are generally made on fertile females while their mates are absent and are marked by male aggression and female resistance behaviors, such as fleeing, hiding, and obstructing the cloaca (McKinney and Evarts 1997). Briskie and Montgomerie (2001) suggest that copulation in passerines is unlikely to be possible without cooperation by the female due to anatomical constraints (male passerines have cloacae rather than intromittent organs, requiring females to adopt a copulatory position for sperm transfer to occur), implying that successful FEPC attempts in passerines indicate female capitulation. McKinney and Evarts (1997) note that some researchers have reported successful FEPC in passerines (without the consent of the female), and it may be the case that even if males cannot physically force females, they can be so persistent in their harassment that at some point it is adaptive for the female to give into reduce costs (Thornhill and Alcock 1983). Under this “convenience polyandry” model, females of many avian species may sometimes put up with EPC attempts to reduce harassment or injury by males, and so female cooperation does not necessarily indicate a lack of male coercion (Westneat and Stewart 2003; Low 2005). In this light, male anatomy may be less important a determinant of costs to females than male persistence.

### Passerines versus waterfowl

Despite an incomplete account of the frequency and associated behaviors of EPC across bird species, clear patterns can be shown to emerge in passerines versus waterfowl. Presumably, males of both groups seek to maximize the total number of matings, with the crucial difference that males of many waterfowl species are anatomically capable of forcing copulation, whereas most male passerines are probably not. The similarity in strategy does not extend to females, however: female waterfowl, according to the literature, pursue a strategy of unconditional resistance to EPC, whereas females of many passerine species often accept and even solicit EPC (Jennions and Petrie 2000; Griffith et al. 2002; Westneat and Stewart 2003). What accounts for the divergence in female strategies between these groups? The situation is puzzling in light of the fact that female waterfowl sometimes expose themselves to high direct costs by resisting. The widespread assumption in the literature is that female waterfowl do not engage in convenience polyandry when costs are very high, but if this is the case, then why do not they? If females never accept EPC, then unconditional resistance must result in higher average fitness for females than a strategy of conditional resistance. In order to evaluate the pressures that may have led to the evolution of this perplexing behavior, I will first consider the costs and benefits to females of engaging in EPC and then examine how these may differ between waterfowl and passerines in a way that might account for their diverging strategies.

### Costs to females of EPC/costs of mating

As discussed above, a female waterfowl that resists EPC may expose herself to a high risk of injury or death. But although resistance to mating can be risky for female waterfowl, mating itself is predicted to be costly for individuals of any species, and particularly for females, who typically have less to gain by each subsequent mating than do males (Bateman 1948; Trivers 1972; Holland and Rice 1998). These costs may apply not only with extrapair males but also for pair copulations, and so a female may benefit by reducing mating frequency with her social partner as well as with other males. Mating can

impose costs on females through increased risk of predation, energy and time expenditures, exposure to parasites or sexually transmitted diseases, and the possibility of injury by the male (Jennions and Petrie 2000). These costs may increase when males have intromittent organs, such as in waterfowl, as discussed below. Male postcopulatory mechanisms can impose costs on females as well, such as manipulative or injurious seminal substances, chastity plugs, and mate guarding behaviors that have evolved as male strategies to reduce female remating frequency and thereby minimize sperm competition (Stockley 1997). Among species in which females seek out multiple mating opportunities, searching for suitable mates can be time and energy consuming and can expose females to predation through increased visibility and decreased vigilance (Jennions and Petrie 2000). In socially monogamous birds, pursuing multiple mating opportunities carries the risk for the female of being caught by her mate, which could result in a reduction in paternal care for her offspring or abandonment by her mate (Afton 1985; Birkhead and Møller 1992), as well as the possibility of punishment by her mate, which has been modeled by Clutton-Brock and Parker (1995) and documented, for example, in the lesser gray shrike *Lanius minor* (Valera et al. 2003).

### Benefits to females of EPC

Given that at least some of the aforementioned costs should apply to any female bird that pursues EPC, it is appropriate to ask why females of many passerine species commonly seek out multiple mating opportunities. Griffith et al. (2002) reviewed hypotheses for the function of female pursuit of EPC, including suggestions that EPC guards against infertility of the social mate, increases genetic diversity among offspring, allows the female to obtain good genes for her offspring, and allows the female access to nongenetic resources held by extrapair males. Griffith et al. (2002) found insufficient empirical support for any of these hypotheses. In addition, Westneat and Stewart (2003) showed that extrapair paternity, as well as female and male pursuit of EPC, varies considerably among species. Taken together, there is little basis at this point for making generalizations about the function of EPC across avian species (however, for factors that may help explain patterns of interspecific variation in extrapair paternity, see Griffith et al. 2002).

Studies in other organisms can also help to shed light on the evolution of female acceptance or solicitation of EPC. Byrne et al. (2008) found that female fruit flies *Drosophila melanogaster* expose themselves to male harassment, and thus mate multiply, only when males are associated with an important food resource. In this system, females face well-documented fitness costs such as reduced life span resulting from elevated rates of mating (Chapman et al. 1995), but when avoiding males comes at the cost of acquiring nutrients, females may choose to expose themselves to a higher mating frequency than is necessary for fertilization. In this sense, females might accept multiple mating, or EPC, not because they benefit but because the costs of avoiding males are high.

Although females of different species may have very different reasons for pursuing or accepting EPC, it seems clear that there must be a fundamental difference in the cost-benefit analysis for female passerines and waterfowl. Whereas the female waterfowl behavior of unconditional resistance to EPC is perplexing from the standpoint of convenience polyandry, as discussed above, the comparison with passerines makes the waterfowl strategy even more difficult to understand from an evolutionary perspective. Is it that female passerines have more to gain from EPC than female waterfowl? Is it that female waterfowl have more to lose? Below, I consider 5 hypotheses

that might account for this apparent enigma and examine each hypothesis from the standpoint of whether it can explain why female waterfowl would risk injury and death to resist EPC, as well as whether it can account for the difference between the strategies of female waterfowl and female passerines.

### Incomplete evidence

#### *Female waterfowl resistance to EPC is not unconditional*

Despite minimal evidence of female consent, it is possible that female waterfowl sometimes consent to EPC with particularly manipulative males to reduce costs (i.e., convenience polyandry). This could happen, for example, if female waterfowl only accept EPC in areas of dense vegetation, where mates (and also researchers) would be less likely to observe them (Birkhead 1987; Sorenson 1994a). A study by Tryjanowski et al. (2007) of the great gray shrike *Lanius excubitor*, a passerine species, found that both males and females choose more secret locations for EPC than for pair copulations, and the same could be true in some species of waterfowl. The hypothesis that female waterfowl only consent to EPC when well hidden would be difficult to prove for obvious reasons, and it might be unlikely in many waterfowl species because they tend to occupy open habitats, where it would be difficult to hide an EPC (Sorenson 1994b).

Nonetheless, there is no evidence that female resistance to FEPC is a fixed behavior. McKinney et al. (1983) note that female lesser snow geese, while incubating eggs on the nest and in the absence of their mates, were seen to put up no resistance to extrapair males, most likely to avoid a scuffle which might result in broken eggs. Sorenson (1994b) reports 2 cases in which female white-cheeked pintails did not appear to resist FEPC attempts. Both occurred on the ocean while the females' mates were absent, and the author suggested that the females might have given in to the males because the dangers posed by the ocean waves and currents increased the costs of resistance. The ability of a female to assess the costs of resistance in a given situation and alter her behavior accordingly suggests that a form of convenience polyandry may occur on rare occasions and indicates that resistance has not evolved, for example, as a fixed response to conspecific attack. This assertion is supported by the observation that when females are subjected to FPC, they do not resist as vigorously as with FEPC and do not tend to employ escape tactics as with FEPC.

Given the difficulty for researchers of observing an FEPC from start to finish in some species (McKinney et al. 1983), it is also possible that females of some species always resist initially in order to gauge the vigor of the male. If she determines that resistance will be fruitless or too costly, perhaps she ceases or reduces resistance. It is also possible that females sometimes miscalculate either their own resistance ability or the male's persistence, and perhaps, these miscalculations result in the severe injuries or deaths occasionally reported. On the other hand, given that most reports of FEPC are from crowded, heavily male-biased populations, it could be the case that even if females do cease resisting when costs are high, the behavior of the female in some contexts has little bearing on her chances of being injured. For example, if a female is being harassed by multiple males, she may sustain injuries simply by being at the center of a group of aggressive males, and so perhaps in certain contexts, it is not resistance that exposes females to injury but rather an abundance of male aggression.

#### *The risks posed by resisting are not as significant as generally assumed*

Another area in which the evidence in the literature may be incomplete relates to the degree of risk females typically face by resisting FEPC. As noted above, reports in the literature of injury or death resulting from FEPC are almost always anecdotal

and are often made in crowded park populations that tend to have a heavy male bias.

One study measuring mortality in about 2250 radio-marked female mallards in the Prairie Pothole region of Canada from 1993 to 1998 found that while weekly survival probability was fairly low during the most intensive 5 weeks of the nesting period (estimated at 0.625 at the lowest extreme), mortality was largely attributed to predation of females on the nest (Devries et al. 2003). Devries J, Arnold T, Emery B (unpublished data) found that based on a long-term data set on about 3600 radio-marked female mallards in Canada, no mortalities or injuries were recorded as being suggestive of FEPC. However, Devries J, Emery B (personal communication) note that it can be difficult to attribute mortality to a specific cause when monitoring free-ranging birds, and some of the carcasses may have been scavenged before they could be collected. Arnold T (personal communication) notes that many of the studies that report female injury resulting from FEPC occur in highly modified habitats with limited escape cover and suggests that the risks posed to wild mallards from resisting FEPC may be low. He cautions against generalizing anecdotes from crowded park populations to wild populations. Reynolds M (personal communication), who has studied Laysan teal on Laysan Island in Hawaii, reports that female harassment from unpaired males is noticeable, but females are typically paired and males tend to successfully defend their mates. Reynolds has found females that died of trauma, apparently from FEPC, but has not observed any FEPC in progress and notes that small islands are very susceptible to density-dependent population effects, so the sex ratio skew and thus the frequency of forced copulation may change over relatively small time periods.

Given these observations, it seems reasonable to suggest that the combination of female escape behavior and male mate guarding is often sufficient to make the risks for females in wild populations of resisting FEPC fairly low. If this is the case, perhaps there has been little selection on females to engage in convenience polyandry.

If the incomplete evidence hypothesis is true and female waterfowl resistance to extrapair males is not unconditional (i.e., if they practice convenience polyandry when costs are very high) or if resistance is in fact not very risky in wild populations, then the behavior is less perplexing from an evolutionary perspective. However, this hypothesis does not offer much insight into the generalized difference between female waterfowl and female passerines—from a comparative perspective, it still appears as if the latter group tends to garner greater benefits from EPC or else face fewer costs, because female passerines commonly accept EPC while female waterfowl do not. The remaining hypotheses may offer greater insight into the divergent strategies.

### Reinforcement of original mate choice

It is common among waterfowl species for mate assessment and pair-bond formation to take place well before the start of the breeding season (Rohwer and Anderson 1998). In addition, sex ratios among adult waterfowl tend to be male biased (Blums and Aivars 1996), which likely allows females to control mate selection on the wintering grounds (Hohman and Ankney 1994). Females should thus have a reasonable probability of obtaining a desirable mate and might resist extrapair males if they consider themselves to be mated to a high-quality male (Westneat et al. 1990). Brennan P (personal communication) suggests that this, paired with the fact that females may have little opportunity to evaluate the quality of extrapair males outside of normal courtship, might account for the female waterfowl strategy of unconditional resistance to EPC.

Sorenson (1994b) considered the idea that females may resist all extrapair males to avoid mating with a male of inferior or indeterminate quality but rejected the idea for the wild population of white-cheeked pintails she studied. Sorenson (1994b) points out that if the function of female resistance is to avoid mating with males of inferior quality, then females should accept EPC with some males and not others, but this has not been found. Sorenson (1994b) reports that male quality, assayed as mate guarding ability, varied greatly among male white-cheeked pintails, and yet, females did not appear to reduce resistance with higher quality males. Cunningham (2003) reports similar results in a captive population of mallards, in which males were ranked based on female preference, but male rank had no detectable effect on female resistance efforts. I argue that if females stand to gain by mating with high-quality males, then both EPC and the ability to assess quality of extrapair males should be favored for females when paired with suboptimal males. It is possible that the way females “assess” male quality is by resisting all males to screen for the most manipulative (see below).

I argue that the reinforcement of original mate choice hypothesis is not likely to explain why female waterfowl do not appear to practice convenience polyandry—even if a female is paired to the best possible male in the population, surely the costs of mating with an inferior male are sometimes lower than the risk of sustaining serious injuries or even being killed due to resistance. However, the hypothesis may help to shed some light on the difference in behavior between waterfowl and passerines. Given that adult waterfowl populations tend to be male biased, it is possible that a female waterfowl has a better chance than a female passerine of obtaining a high-quality mate, and therefore, the potential genetic benefits of engaging in EPC may be lower on average for waterfowl (for a review of adult sex ratios in wild bird populations and evidence that anseriform populations tend to have an adult sex bias that is more male skewed than in passerines, see Donald 2007).

On the other hand, Griffith and Immler (2009) apply the concept of a genetically loaded raffle (Ball and Parker 2003) to EPC behavior in birds and suggest that females might benefit from mating with extrapair males that are not necessarily more attractive or even phenotypically different from their social mate, as multiple mating may allow the female to select the most genetically compatible sperm. EPC is predicted to result in no extrapair paternity if the extrapair male is less compatible than the social male (Griffith and Immler 2009). In this light, EPC can be viewed as an insurance policy against genetic incompatibility, or perhaps infertility, of the social male. There is some recent empirical evidence to suggest that females might pursue EPC for this reason. In the Gouldian finch *Erythrura gouldiae*, a passerine species, females use male coloration as a proxy for genetic compatibility and mate preferentially with males displaying the compatible color morph (Pryke and Griffith 2007). However, Pryke S, Rollins LA, Griffith S (unpublished data) found that even when paired with a male of the compatible morph, females will solicit EPC from males of the inferior morph when no other males are available. Although Pryke S, Rollins LA, Griffith S (unpublished data) found that these extrapair males were shown to sire no offspring, the fact that females solicited EPC with a male less attractive than her own mate suggests that EPC may serve an insurance function in this system. Applying this logic to waterfowl suggests that females might benefit from EPC, even when extrapair males are of lesser or unknown quality. However, 1 study in mallards (Denk et al. 2005) found that sperm quality, rather than genetic compatibility (measured as degree of relatedness), determined fertilization success among competing ejaculates.

I suggest that the hypothesis that female resistance has evolved to maintain control over mate choice may be bolstered with the addition of a certain key piece of information, namely, whether females can exert postcopulatory control over fertilization, which is not yet known for waterfowl. Many birds, including passerines, are able to eject sperm after copulation with an undesirable male (Gowaty and Buschhaus 1998; Briskie and Montgomerie 2001). Female feral fowl, *Gallus gallus domesticus*, a species of Galliformes, in which males are larger and able to coerce females, have been shown to eject sperm of subdominant males (Pizarri and Birkhead 2000). Sperm ejection ability may reduce the costs of convenience polyandry in these species because a female is unlikely to relinquish choice in the paternity of her offspring by mating with less preferred males. Some authors (Wagner R, Gowaty P, personal communication) suggest that sperm ejection is likely in waterfowl but would be difficult to observe as it could be mistaken for defecation and because copulation occurs on water. Brennan et al. (2007) hypothesize that the vaginal pouches in waterfowl revealed in their morphological study might trap sperm nearer the entrance of the vagina, perhaps making it easier for the female to eject. However, others suggest that sperm ejection ability might be less likely in waterfowl because the male intromittent organ allows for sperm transfer to occur inside the vaginal tract, where it may be difficult for a female to manipulate (Briskie and Montgomerie 1997; Denk 2005).

Sperm ejection is not the only way in which females may exert postcopulatory control over fertilization. Females of some animal species may be able to bias sperm use in favor of preferred or less related genotypes (reviewed in Cunningham and Cheng 1999), but 1 study in mallards found that although females tended to use sperm of 1 genotype over another, they were not consistent in their preference (Cunningham and Cheng 1999). Future research into the ability of female waterfowl to eject sperm or exert some other means of postcopulatory control over fertilization is needed. If female waterfowl were found to lack such control, this difference with passerines might play a role in explaining the difference in resistance behaviors between the 2 groups.

### Maintenance of the pair-bond

Sorenson (1994b) suggested that a strategy of unconditional resistance to FEPC in female waterfowl may have evolved to avoid desertion by her social mate and thereby the loss of protection and territory defense provided by the male (McKinney 1985; Cunningham 2003). Afton (1985) describes a focal female lesser scaup, *Aythya affinis*, whose mate reduced defense and eventually abandoned her after she was subjected to more and more FEPC over the course of the breeding season. This same female later abandoned her nest 3 days after beginning incubation. Evarts S (personal communication) also reports unpublished observations of mate abandonment after FEPC in mallards. Although these cases suggest that the costs of mate abandonment are probably considerable for females, few reports of mate abandonment in waterfowl are available in the literature, and it is unclear how often males that witness their mates involved in FEPC really abandon them.

Sorenson (1994a) reports female white-cheeked pintails abandoning their nests after being subjected to many FEPC attempts, although no mate abandonment or reduction in mate guarding was reported in this study. Sorenson (1994b) suggests that these females may have suffered from reduced mate guarding after their mates witnessed extrapair males forcing copulation with them, but it is also possible that the males were simply poor mate guards to begin with.

I suggest that the maintenance of the pair-bond hypothesis is compelling in its ability to explain why accepting EPC might be risky for female waterfowl, but it is not sufficient to explain a female strategy of “unconditional” resistance. Although the costs of mate abandonment can be very high—particularly when females are reliant on their mates to guard them from extrapair males—a female being subjected to a particularly aggressive FEPC seems likely to lose more fitness by continuing to resist than she would if she ceased resisting to reduce the likelihood of injury or death, even if she risked mate abandonment as a result.

In addition, the recent study of male and female genital coevolution in waterfowl (Brennan et al. 2007) suggests that maintaining a mate’s investment is not the only factor that has influenced the evolution of female waterfowl mating strategy. If the vaginal structures revealed in that study indeed function to thwart unwanted fertilization, they could not have evolved to do so for the benefit of the female’s mate, who will have no way of knowing the fate of the sperm from a successful FEPC. Males should be selected to reduce parental investment whenever their paternity is called into doubt—usually after witnessing an EPC (Westneat et al. 1990)—so the advantage the female gains by postcopulatory control over fertilizations must be independent of pair-bond maintenance considerations.

Lastly, the argument that the risk of mate abandonment drives unconditional resistance behavior in female waterfowl could be seen as dubious from a comparative perspective. In passerines, male parental investment is crucial in many species, in which males share incubation and feeding responsibilities, and chicks are entirely reliant on their parents until fledging. In waterfowl, males provide important aid to the female during breeding, and mate guarding is often crucial for breeding success, but it is not clear that the risk of losing a mate is greater for female waterfowl than it is for female passerines. If unconditional resistance to EPC has evolved in waterfowl to reduce the risk of mate abandonment, why has not a similar strategy evolved in passerines? One possibility is that females only accept or pursue EPC in passerine species in which male care is not crucial to offspring survival. There is some evidence that this may in fact be the case, as suggested by the finding that interspecific rates of extrapair paternity, across several avian groups, tend to be negatively correlated with the need for paternal care (reviewed in Griffith et al. 2002). However, Griffith and Immler (2009) caution that rates of extrapair paternity in a population may bear little relation to rates of EPC and thus should not be used as a proxy for female mate fidelity.

### Minimization of mating costs

The presence of an intromittent organ in waterfowl may indicate that mating itself is likely to carry higher direct costs for females than it does in passerines, which lack an intromittent organ. Briskie and Montgomerie (1997) note that the intromittent organ exposes both sexes to an increased likelihood of contracting a sexually transmitted disease, and there is ample evidence that sexually transmitted diseases in waterfowl pose a serious risk in terms of female fitness (reviewed in Cunningham 2003). In addition, intromittent organs have been implicated in damage to the female reproductive tract and a reduction in female immune function (reviewed in Arnqvist and Rowe 2005). Cunningham (2003) tested hypotheses on the function of resistance to EPC and suggested that, given the added mating costs that an intromittent organ poses to female waterfowl, unconditional resistance may have evolved to avoid copulation and therefore reduce costs of mating.

From a comparative perspective, I suggest that the minimization of mating costs hypothesis can go a long way in explain-

ing the difference between waterfowl and passerine behavior. As discussed above, mating in general is predicted to carry higher net costs for females than for males. But this, in addition to the fact that mating might be particularly costly in female waterfowl, suggests that female waterfowl resistance to EPC is perhaps not surprising. Female passerines likely still face some costs from mating, but if these are low enough, the benefits of EPC might more than compensate.

However, although a certain degree of resistance should be expected in waterfowl on the basis of these increased costs, a strategy of unconditional resistance remains unexplained by the current hypothesis. The premise that females always resist extrapair males to reduce mating costs rests on the assumption that the costs of mating are always higher than the costs of resisting. However, the costs of both mating and resisting are dynamic and change with time and circumstance. These costs depend on traits that vary among individuals, such as body size and reproductive state of both the male and female, as well as extrinsic variables such as nutrition (Blanckenhorn et al. 2007). When resistance fails, the female must pay both the costs of struggling and mating (Arnqvist 1992), so resistance can be a risky strategy as well as a costly one. In certain cases, the costs of resistance are necessarily higher than the costs of mating. As described above, females have been reported to sustain serious injuries and sometimes even die as a result of resistance to FEPC. If a female waterfowl response to extrapair males had evolved to reduce direct costs, it would have to be a flexible strategy whereby females would resist when the costs of mating are higher than the costs of resistance and cease resisting when the reverse is true.

Arnqvist (1992) predicted that when female resistance functions to minimize costs, the level of resistance should be negatively correlated with the abundance of harassing males, so that as male harassment increases females become less reluctant and mate more frequently. This is essentially convenience polyandry, whereby females consent to mating to reduce the costs of resistance. Increased male harassment occurs fairly often in waterfowl, as when multiple males chase a single female, which has sometimes been shown to increase the risk of injury to the female (McKinney et al. 1983), but females have not been observed to reduce resistance in such situations (McKinney and Everts 1997). Therefore, current knowledge of female behavior is inconsistent with a convenience polyandry scenario, suggesting that if female resistance is indeed unconditional, the unconditional nature of it has not evolved as a way for females to minimize costs.

### Resistance as mate choice

Despite the apparently high direct costs of unconditional resistance, I argue that a female might use unconditional resistance to screen males so that only those capable of overcoming her defenses succeed in mating with her (Christoleit 1929a, 1929b), and the indirect benefits gained from this could play a role in the evolution of waterfowl mating systems (Cunningham 2003). The idea that a system of ostensible sexual conflict—marked by male manipulation and female resistance—may in fact imply indirect benefits to females through the production of manipulative or genetically high-quality offspring has been the subject of significant controversy (e.g., see Cordero and Eberhard 2003; Hosken and Tregenza 2005). However, the debate has centered on the potential for indirect benefits to outweigh direct costs, an idea which is not only difficult to test (but see Orteiza et al. 2005) but also fairly improbable for theoretical reasons (Kirkpatrick 1996) and particularly unlikely in groups such as waterfowl in which resisting FEPC has been shown in some cases to have very high direct costs for females. What I am suggesting then

is not that female waterfowl have net gains from FEPC but rather that the indirect benefits of resisting all EPC to screen for high-quality males might reduce the net costs for female waterfowl such that a strategy of unconditional resistance may have evolved as a way for females to “make the best of a bad job.” In other words, given that females cannot avoid male harassment and must therefore pay the apparent net fitness costs resulting from either mating or resisting FEPC, selection should favor unconditional resistance over convenience polyandry if this results in indirect benefits that, on average, partially offset the risks of resisting FEPC and thereby reduce the net fitness costs incurred. Given that costs of mating, such as exposure to sexually transmitted diseases or risk of mate abandonment, may be considerable for female waterfowl, these costs may select for a high level of resistance, which could kick start a process by which unconditional resistance is eventually favored. As this argument does not rely on net benefits to females and does not imply a lack of sexual conflict, I suggest it is not subject to the same objections as claims about cryptic female choice driving systems of ostensible conflict (e.g., Cordero and Eberhard 2003). Additionally, the idea that indirect benefits may “offset” but not necessarily “outweigh” direct costs is probably more in line with the early sexual selection literature on this topic. Notably, Parker (1979) pointed out that “the possible benefits which accrue to females via sons which inherit the sexual selection advantages of their fathers . . . [may] reduce the extent of the [intersexual] conflict” (p. 130).

The resistance as mate choice hypothesis is an example of “indirect mate choice” (Wiley and Poston 1996) and is similar to the “resistance as a ploy” hypothesis of Westneat et al. (1990), who suggests that a female’s resistance may either test male quality or else incite male–male competition to encourage the strongest male to mate with her (Christoleit 1929a, 1929b). For a female waterfowl, unconditional resistance may be a way of biasing paternity toward the most manipulative males—perhaps manipulative both in their ability to overcome the female’s behavioral defenses, as well as her complex vaginal morphology, which may function as an anatomical “screen.” This idea can go some way to explaining why female waterfowl do not appear to employ convenience polyandry—the indirect benefits of screening males may reduce selection on females to give in to male harassment. However, despite minimal evidence, it is possible (as discussed above) that females do indeed give in when costs are particularly high or males are particularly manipulative: a female that gives in at the last minute to a very manipulative male has still screened him by her initial resistance—whether she resists to the bitter end or relents to reduce costs should have no bearing on the genetic benefits she will likely secure for her offspring.

Females may gain indirect fitness from screening males through “sexy sons” benefits, if the ability to force copulation is heritable. A female that resists all males allows only those in the population that are best at forcing copulation to mate with her, thus securing the genes for sons that will also be good at forcing copulation and are likely to provide the female with more grand-offspring. Alternatively, a male’s ability to force copulation may be a sort of handicap—an honest signal of good quality—whereby only certain males (perhaps, e.g., those with genes for effective parasite resistance; Hamilton and Zuk 1982) have enough resources to devote to the energetic pursuit of forcing copulation and overcoming the female’s defenses. This “good genes” benefit could apply to both male and female offspring.

I argue that the resistance as mate choice hypothesis is attractive in its ability to both account for the apparently unconditional resistance behavior of female waterfowl and, from a comparative perspective, to explain the difference between

waterfowl and passerines, as follows: From the standpoint of resistance as mate choice, the crucial difference in these 2 systems might be the male ability to force copulation with females. In passerines, in which males of most species probably cannot force copulation, the males in the population with the highest breeding value for fitness tend to be those with the most conspicuous displays. A female passerine can secure genetic benefits for her offspring simply by mating with the most “attractive” males. In waterfowl, however, the males with the highest breeding value for fitness might be those best at forcing copulation. (e.g., Sorenson (1994a) found that in a marked population of white-cheeked pintails, males varied considerably in their ability to achieve FEPC but that a few “high-quality” males were successful at FEPC and also proficient mate guarders.) Therefore, in order to bias paternity toward the best males, a female waterfowl may resist all extrapair males to screen for the most manipulative.

One study (Cunningham 2003) provides some empirical evidence against the resistance as mate choice hypothesis. Cunningham (2003) explored experimentally the idea that female resistance selects for the best males in a population by first ranking males based on female preference and then observing interactions between females and extrapair males of varying rank. Cunningham (2003) found that although females consistently preferred certain males in the population, preferred males were no more successful at forcing copulation than nonpreferred males—there was no difference between preferred and nonpreferred males in time to initiate a copulation and time to achieve intromission. In addition, female resistance was shown to be effective in reducing the likelihood of successful copulation. These results suggest that female resistance, although effective, does not bias paternity toward the most attractive males, and the author (Cunningham 2003) concluded that the function of resistance was not to select for the best males but instead to reduce mating costs. However, as the author points out, there is no evidence that the most attractive males are those best at forcing copulation. A female might look for particular traits in a mate that have little to do with the ability to force copulation, and yet, she might still gain indirect fitness by mating with a highly manipulative extrapair male.

The suggestions from Cunningham’s (2003) study may be bolstered with future work on larger populations that would eliminate some of the potentially confounding factors. For example, perhaps there was little variability among the 13 males in the study in their ability to force copulation, and this may not be representative of a larger, wild population. Moreover, this portion of the study was undertaken with a captive population, and assays were carried out in enclosures, preventing females from flying away. Although captive studies are often necessary to test ideas experimentally and have proved very informative on particular questions in this system, I suggest that in this case, captivity may have denied females a major element of resistance, that is, the ability to escape. However, Cunningham (2003) also collected data on a wild mallard population and, taking pair status as a measure of female preference, found no difference between preferred and nonpreferred males in FEPC success rate, but the sample size (8 successful males achieving 10 FEPC) was small. A larger sample size and, as Cunningham (2003) suggests, a comparison between the fitness of pair and extrapair offspring would be very informative in determining whether indirect benefits play any role in female resistance behavior.

Another potential objection to the resistance as mate choice hypothesis is that sexually antagonistic fitness effects could negate the indirect benefits of mate screening for females. Even if attractive males tend to sire attractive sons, these benefits might be negated if the same genes reduce fitness in daughters, which would limit the possibility for indirect



benefits to drive selection on female resistance. Pischedda and Chippindale (2006) show that in the fruit fly, high-fitness mothers tended to produce high-fitness daughters and low-fitness sons, whereas high-fitness fathers produced low-fitness daughters and did not pass on their fitness to sons, probably because the traits in question were X-chromosome linked. Sexually antagonistic fitness variation has been shown in birds (Brommer et al. 2007), but in the avian ZW/ZZ chromosome system, males (ZZ) inherit the paternal Z-chromosome and are expected to inherit their fathers' attractiveness, which might offset some of the negative association between male attractiveness and fitness of daughters (Pischedda and Chippindale 2006).

I suggest that the resistance as mate choice hypothesis can help to explain the difference between waterfowl and passerine behavior from an extrapair mate choice perspective. Due to the presence of FEPC in waterfowl mating systems, female waterfowl cannot ensure monogamy even if they want to because resistance can sometimes be overcome by manipulative males. What resisting might provide for female waterfowl is a mechanism for choosing among extrapair males. Put another way, both female passerines and female waterfowl probably gain some indirect benefits from EPC, as well as from being choosy about their extrapair mates, but it may be the case that the act of exerting mate preference results in 2 female strategies that look very different from each other. On this basis, I predict that the presence of forced copulation will result in selection for unconditional female resistance to extrapair males, whereas a lack of forced copulation will select for female acceptance of EPC in order to allow females in either system to bias paternity toward extrapair males with high breeding value for fitness.

The presence of forced copulation in hihi and the lack of forced copulation in some species of waterfowl means these species provide potentially informative exceptions to the rules in these systems. Based on the prediction that the presence of FEPC in a mating system will determine female resistance behavior, we should expect to find hihi females resistant to all EPC and females of waterfowl species without forced copulation amenable to EPC.

Consistent with this prediction, Low (2005) reported that female hihi were never observed to solicit or initiate EPC. In a population containing 50 female hihi, all primary paired females resisted FEPC attempts, whereas 5 secondary females of polygynous males were reported to mate without resistance with a nearby neighbor. However, Low (2005) believes that unconditional resistance in primary paired hihi females functions to minimize the risks of EPC rather than screen males.

Among waterfowl, swans are often considered highly monogamous. No FEPC has been reported in any of the 7 species of the swan tribe Cygnini (McKinney and Evarts 1997), and so evidence of EPC in these species would be telling. Interestingly, a paternity study of black swans *Cygnus atratus* found that 10–17% of young were the result of extrapair paternity and 27–40% of broods contained at least 1 extrapair offspring (excluding the <5% of cygnets determined to be the result of intraspecific brood parasitism), despite the fact that males do not force copulation (Kraaijeveld et al. 2004). Thus, swans provide an example of waterfowl that lack FEPC, in which females must sometimes accept EPC, as predicted.

## CONCLUSIONS

The belief, widespread among researchers, that females unconditionally resist FEPC in waterfowl presents a significant paradox: unlike in passerines, female waterfowl never appear to accept EPC, but the purported inflexibility of this strategy sometimes exposes females to very high direct costs and would

seem to preclude females from reaping the theoretical benefits of EPC. The idea that female waterfowl never consent to FEPC may be overstated, as there are a few anecdotes in the literature in which females have been observed to put up no resistance when costs of resisting are very high, consistent with a convenience polyandry scenario. In addition, some authors who have worked on wild populations of waterfowl suggest that the risks of FEPC to females are highly context dependent, and observations from crowded urban populations should not necessarily be considered representative of more natural populations.

Hypotheses that seek to explain unconditional resistance behavior from the standpoint of reinforcing original mate choice, reducing mating costs, or minimizing the risk of mate abandonment go a long way to explaining habitual resistance to EPC in female waterfowl but fail to explain the observed pattern of unconditional resistance, as females should theoretically engage in convenience polyandry whenever the costs of resistance outweigh the costs of mating itself or its consequences. Although the pair-bond maintenance hypothesis has been considered the most compelling explanation for this behavior (McKinney and Evarts 1997), it is called into question by the recent discovery of complex genital coevolution in this species, which appears to function in females to thwart forced fertilization attempts by males. As males have no way of knowing whether the sperm from successful FEPC on their mates will result in fertilization, females are unlikely to have evolved internally resistant morphology in order to maintain their mates' assurance of paternity.

Although it is likely that female waterfowl experience net costs as a result of FEPC, I suggest the indirect benefits from screening males should be considered in this system for their potential to reduce net costs and make the unconditional resistance strategy, on the whole, the least costly choice for females. An examination of female strategies in relation to EPC in both passerines and waterfowl reveals a pattern of female acceptance of EPC in the absence of forced copulation and female resistance to EPC in the presence of forced copulation. This is consistent with the prediction of the resistance as mate choice hypothesis, and I suggest that waterfowl present a promising system for further study of the potential for indirect benefits to play a part in driving selection on female resistance behaviors.

There are many interesting questions that need to be answered: Is the male ability to force copulation heritable? Do extrapair offspring have differential fitness from pair offspring? How often does mate abandonment really occur? Does female behavior in response to FEPC attempts differ subtly among males, as a function of male vigor or genetic quality? Do female waterfowl engage in a cryptic form of convenience polyandry? The answers to these questions, and many others, will help to shed light on the evolution of female strategies under sexual conflict.

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