

Ultimate Causation of Aggressive and Forced Copulation in Birds: Female Resistance, the CODE Hypothesis, and Social Monogamy¹

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SYNOPSIS. Except in ducks and geese (Anseriforms), aggressive or forced copulation in birds is rare. The rarity of forced copulation in birds theoretically is due to morphological and physiological mechanisms of female resistance that place fertilization most often under female control. Traits theoretically associated with resistance by females include: digestive epithelium lining the section of the cloaca receiving sperm and powerful cloacal musculature used to eject contents, including waste material and sperm. These traits suggest that the Immediate Fertilization Enhancement Hypothesis may be an inadequate ultimate explanation for forced copulation when it occurs. Ideas in Heinroth (1911) and Brownmiller (1975) suggested an alternative, the CODE Hypothesis, which says that aggressive copulation creates a dangerous environment for females. This, in turn, fosters male mating advantage via social monogamy, because selection sometimes favors females who trade sexual and social access for protection from male aggression. Thus, theoretically, “trades” of protection for copulation favor the evolution of social monogamy even in species with little or no paternal care. Individual males may accrue selective advantages through direct benefits, kin-selected benefits, or reciprocal altruism. The CODE hypothesis for social monogamy predicts variation in extra-pair paternity from preferred mates, variation in male reproductive success, and variation among females’ post-insemination resistance mechanisms as functions of variation among females’ vulnerabilities (ecological and intrinsic) to aggressive copulation. Observers will base intraspecific tests on variation among females in their vulnerabilities to male aggression against them.

INTRODUCTION

Evolutionary (ultimate or functional) hypotheses predict behavioral, physiological, and morphological traits

Darwin (1871) posited that sexual selection accounted for bizarre and elaborate traits that were difficult to explain through natural selection (Darwin, 1959). His questions had to do with the origin and maintenance of traits, and his questions determined his method (Ghiselin, 1974). He was trying to explain recognized traits through the then novel explanations for evolutionary change and stasis, natural and sexual selection. Today it is no longer necessary to convince others that natural or sexual se-

lection occurs, or that selection provides a cogent and reasonable explanation for many biological phenomena (Reeve and Sherman, 1993). Part of Darwin’s legacy is that theoretical regularities in selection pressures predict existence of so-far unobserved traits (within the limits of available variation and constraints on adaptation).

This turned-around method of predicting traits from theoretical selection pressures necessarily integrates studies of ultimate and proximate causation. An example is from Trivers (1972). He argued that even in monogamous species males would be under selection not only to cooperate in the care of offspring with one female, but to seek fertilizations with other females. He expected such selection to be relatively strong because the primary limiting resource for male reproductive success is access to mates. He assumed regularities in selection pressures in sexual species given regularities in the ecological problems conspecifics

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create for each other. He then predicted never-before-observed behavioral variation, including mate-guarding and extra-pair paternity in socially monogamous species. In response, empiricists rushed to discovery. Behavioral variation consistent with the functional explanation of mate-guarding occurs in almost all examined species of birds (e.g., Gowaty *et al.*, 1989; Birkhead and Møller, 1992); and, it is now clear that in most socially monogamous species extra-pair paternity occurs (Birkhead and Møller, 1992; Gowaty, 1996a, b). For mate-guarding and extra-pair paternity the fit of observation to prediction was good, and the search for never-before-observed traits increased our understanding of social behavior.

In addition, observation of never-before-observed traits suggests new questions. For example, what are the proximate causes of extra-pair mating by females? Buschhaus (1997) has begun to answer this question with her report showing levels of estradiol in blood serum of fertile female eastern bluebirds, *Sialia sialis*, was significantly positively correlated with the strength with which their territorial partners guarded them. This is an intriguing observation because we already know that males mate-guard most strongly females who extra-pair mate than females who do not (Gowaty and Bridges, 1991).

Another example of the potential for rich pay-offs from the "prediction-of-traits-from-selection-pressures" approach comes from the work on human sexual behavior by Baker and Bellis 1993a, b; 1996. Though many will doubt their claims until careful replication by other workers. Baker and Bellis already have revolutionized the study of human mating behavior by their use of the Sperm Competition Hypothesis. This hypothesis guided these researchers to look at under-investigated phenomena suggested by the Sperm Competition Hypothesis, which predicted, among other things, an adaptive function to female masturbation, which in turn led to first-time documentation of the orgasmic "dancing cervix." As long as the only hypothesis guiding explorations of the anatomy and physiology of human sex was that reproductive

traits served to facilitate pregnancy and childbirth, researchers and others failed to note some of the most interesting behavioral, morphological, and physiological variations in women. The Sperm Competition Hypothesis may not be the only functional explanation for newly observed traits in women such as those that block pregnancy, inhibit fertilization success, or affect differentially the success of sperm from different males, but the idea motivated the evaluation of the predictions that lead to documentation of fascinating variations never-before-observed systematically in women.

What stimulated this symposium was the historically powerful "levels of analysis" approach (Tinbergen, 1963) to understanding the causes of behavioral traits. In this paper we integrate across these levels by focusing on functional (ultimate) hypotheses to predict behavioral, morphological, and physiological traits, some of which are the proximate causes of other traits. We hypothesize the operation of common selection pressures that arise from the ecological circumstances the sexes create for the reproductive success of the opposite sex. The genius of Trivers (1972), Hamilton (1964), and Fisher (1930) may turn out to be not just that they predicted never-before-observed phenomena, but that they modified Darwin's method, and theorized regularities to selection pressures that predicted the existence of traits whose function was the solution to ecological "problems" faced by individuals.

In this paper we show how predicting trait variation from hypothetical selection pressures affects our understanding of forced copulation and social monogamy at proximate and ultimate levels of analysis. We (1) discuss several recently posited selection pressures and the existence of never-before-predicted traits, (2) describe theoretically their relationship to social monogamy in birds, and (3) predict variation in traits having to do with the dynamics of social monogamy in waterfowl (Anseriformes) and perching birds (Passeriformes). Throughout, we imply how the trait based and selection pressure based approaches illuminate proximate and ultimate causes of traits. We do this by a review of the mor-

phology and physiology of copulation from the perspective of females.

Our paper is structured around Sexual Dialectics Theory (SDT) (Gowaty, 1997), which predicts regularities in selection pressures different from those of standard sexual selection theory. The dynamical nature of SDT begs the question of the effectiveness of forced copulation in birds. After a review of the morphology and physiology of female copulatory organs, we argue that in most, perhaps even, all, birds forced insemination is highly unlikely or even impossible. If this is so, an explanation for forced copulation different from an increase in immediate fertilization success is called for. Thus, we describe an alternative hypothesis of ultimate causation of forced copulation, and a new model of individual dynamics under social monogamy, for the case when males create dangerous environments for females. We discuss predictions in comparison to the more usual ultimate hypothesis that immediate fertilization enhancement for males explains forced copulation. We do not belabour our opening point that novel hypotheses of ultimate (evolutionary, functional) causation may lead to never-before-observed traits and the search for alternative ultimate causes and their proximate correlates.

SEXUAL DIALECTICS

A long overlooked source of selective pressures acting on females and males comes from sexual dialectic theory (Gowaty, 1997). "Dialectic" refers to change through the conflict of opposing forces; in the context in which we are using the term, it refers specifically to sexual coevolution that occurs when opposite sexes create ecological problems that the other sex must solve in order to survive and reproduce. Sexual dialectic theory posits a type of sexual conflict that occurs whenever females differentially prefer certain males with whom they would likely produce high quality offspring, and reject certain other males for matings. Such female choice inevitably sets sexual conflict in motion, because, whenever a female rejects a male, selection should act on that male such that he should attempt to affect a female's reproductive de-

cisions either by advanced salesmanship, manipulation, and aggressive (Smuts and Smuts, 1993) or affiliative coercion. Such males should experience selection to control for their own benefit the reproductive capacities of females. If such males succeed in "changing females' minds," such manipulated females will suffer deleterious fitness consequences, so that selection will favor females that resist control of their reproductive capacities by males. These females will experience selection favoring behavioral, physiological, or morphological resistance mechanisms to reproduction with non-optimal males. (Note that just because certain selection pressures exist, it does not mean that certain traits always necessarily exist. Trait existence is a result of many factors including variation on which selection can act, chance, and conflicting constraints.)

Sexual dialectic theory (SDT) makes a number of predictions, some of which are novel (Gowaty, 1997). For example, it predicts that in typical species (those in which intrinsic limits primarily constrain females' reproductive success in contrast to female access limiting males), females will be facultatively proactive, enthusiastic about mating with some males, and resistant to mating with others. For example, one might imagine that under some circumstances any female might mate without courtship even in species in which elaborate courtship is usual, such as in some *Drosophila* species. Here we are assuming that male courtship (broadly defined as what males do to get females to mate with them) is what rejected males do to get females "to change their minds". In other words, we assume that the information most crucial to females' decisions with whom to share her gametes is available to them without displays from males. The notable aspect of this novel prediction is not that females should vary in their tendencies to mate, nor that some females are "randier" than others, but that females will sometimes be anything but "coy," shy, or retiring about mating with particular males. This prediction is in marked contrast to those derived from more standard characterizations of selective pressures acting on females and males (e.g.,

Bateman, 1948; Eberhard, 1996, pp. 37–38) that lead to expectations that females will be “coy” about mating. As far as we know, no one has attempted a systematic examination for facultatively sexually enthusiastic females in the absence of “courtship” in any species. Sarah Hrdy (1997) and her students (Small, 1993) have often commented on the existence of sexually enthusiastic females in primates and noted that little or no theory exists to explain this unexpected behavior. SDT predicts that facultatively enthusiastic females should exist in all or almost all sexual species and that the progeny from these matings will have higher viabilities than progeny from matings when females are less enthusiastic (Gowaty, 1997).

SDT predicts (Gowaty, 1997) that in natural or experimental situations in which males are unable to manipulate females’ mating decisions, that is, in “free female choice” situations, females will choose mates using evidence of the likelihood of high viability offspring. The hypothesis predicts that in all, or at least most, species some females mate for superior viabilities in their offspring. This prediction differs from other treatments of the problem of why females choose in the expectation that all females are under selection to mate to maximize viabilities of offspring. Of course, females often mate with males because they have no other options for gaining access to resources or due to coercion or manipulation or to other ecological limitations (Gowaty, 1996a). Even in species in which males broker females’ access to essential resources, in which some females may base their choices of mates on the resources the males control, some females will mate with males for superior offspring viability.

SDT predicts that male attempts to control females’ reproductive capacities will be common (Gowaty, 1997). More important, it predicts that females will evolve resistance mechanisms to nonpreferred matings (Gowaty, 1997). So, in species with internal fertilization, if a nonpreferred male succeeds in inseminating a female, selection will favor females able to rid themselves of the sperm of such males. SDT, therefore,

predicts that many so-called sperm “storage” organs are really sperm “management” organs (Gowaty, 1997), often of the sort documented by Eberhard (1996). These may have originated as sites for the destruction rather than for storage of sperm. SDT predicts that in species in which males attempt to coerce females, females will have evolved behavioral mechanisms for ejecting sperm from their reproductive tracts, physiological mechanisms for disarming or denaturing sperm, and/or physiological mechanisms for managing the movement of sperm through their reproductive tracts. Parker’s (1970) sperm competition hypothesis makes similar predictions; one of the chief differences is that the SDT predicts that such mechanisms even may occur without double mating by females, *i.e.*, even in species in which sperm competition is unlikely to occur.

Among our points germane to this symposium is that some attempts to refute or verify the selection pressures that characterize SDT will pivot initially on the observation of novel traits that SDT predicts. The observation of novel traits will then provide the opportunity to evaluate alternative functional explanations for such traits as well as proximate causes of newly observed traits. For example, if contact with mucus in female reproductive tracts sometimes kills sperm as SDT predicts, the proximate mechanisms by which mucus kills sperm will be a new research topic, important for predicting ways that selection can act on males to overcome a female resistance trait.

There are several other implications of this idea that we also want to comment upon. Female resistance mechanisms may account for the notably variable means of post-insemination sperm managing mechanisms (Thornhill, 1983; Eberhard, 1996). Researchers observed these mechanisms of female discrimination (Eberhard, 1996) in the absence of theory predicting their occurrence. Thus, Eberhard calls for a post hoc revision of what males are competing for as an explanation for what he calls “post-insemination discrimination mechanisms.” He says that “sexual selection is better understood as a result of competition among males for access to female gametes

rather than for access to the females themselves" (p. 42). In contrast, SDT (Gowaty, 1997) says that sexual conflict is fundamental to relationships between the sexes, and predicts particular trait covariation (sexual coevolution) in males and females. SDT predicts mechanisms of female discrimination that take place after insemination in those iteroparous species in which males behaviorally coerce mating. Eberhard says that cryptic female choice ensures sexual conflict; in contrast SDT says that sexual conflict ensures the existence of post-insemination mechanisms of female discrimination and furthermore predicts, within some admittedly broad limits, the nature and degree of variation in such resistance traits.

Something that illustrates the dynamical and dialectical nature of these ideas is that successful resistance mechanisms in females, of course, implies the operation of additional selection on males to overcome female resistance mechanisms. Theoretically, female vulnerabilities to types of male manipulation determine the mechanisms available to males for manipulation (see Gowaty, 1997 for a discussion of the co-occurrence of male manipulation options and mating systems). Thus, given appropriate variation on which selection can act, resistance and control mechanisms should co-occur in predictable patterns.

SDT predicts that the mechanisms of male manipulation of females' reproductive decisions will depend on variation among females' intrinsic characteristics or the environments of the females (Gowaty 1996a, 1997), thus, one of its most important components of SDT is that variation among females (Gowaty, 1996b) is central to analysis of its predictions. For example, the SDT approach would suggest that understanding the adaptive significance of penis length in primates is impossible without some corresponding information about vaginal characteristics as well (Brown *et al.*, 1995). This reasoning, furthermore, facilitates prediction of the mechanisms males use to manipulate females' reproductive decisions in various groups of organisms (Gowaty, 1997).

PREDICTIONS OF AGGRESSIVE COPULATION IN BIRDS

Here, in further illustration of the ability of SDT to predict some never-before-observed traits and variation in known traits, we discuss finer-grained predictions about a potential mechanism of male manipulation of females' reproductive decisions, aggressive copulation in birds. This discussion hinges on females' abilities to resist male aggression, thus active female agency is central to the considerations here. This discussion further illustrates the dynamical nature of processes that depend on conflict of opposing forces, that would seem to be intrinsic to much sexual coevolution.

In what follows we call what others call "forced copulations" "aggressive copulations," to be as operational as possible about what counts as forced (Estep and Bruce, 1981).

SDT predicts:

- *Aggressive copulation in birds is more common in species with than without intromittent organs.* In contrast to most vertebrates, in most birds and salamanders males accomplish internal fertilization without an intromittent organ. Fewer than 3% of birds have intromittent organs (Briskie and Montgomerie, 1997). Most species have sexually monomorphic openings to their reproductive tracts known as cloacae. Some males have cloacal protuberances during the breeding season because the seminal vesicles lie near the skin surface at the cloaca, but this protuberance only superficially resembles an intromittent organ. Because cloacae are on the ventral portion of bodies, physical contact must involve male and female cooperation for successful sperm transfer (Fitch and Schugart, 1984). In species with intromittent organs (ratites, tinamous, and anseriformes), sperm transfer would seem not to depend so much on the cooperation of the female as it does in species in which sperm transfer depends on some important level of female cooperation with males. Thus, a male copulatory structure that obviates the need for female cooperation motivates the prediction that ag-

gressive copulation is more likely in ratites, tinamous, the ducks and geese than in passerines. Indeed, McKinney *et al.*, (1983) list almost 50 species of anseriformes with evidence consistent with aggressive copulation, while we were able to find reports for 16 non-anseriform species (Table 1).

- *Aggressive copulation is more common in species in which male morphological structures can restrain females.* Males can restrain females by grasping with their claws or beaks. Thus, all else being equal, SDT predicts that aggressive copulation occurs more frequently among species with robust beaks, as in seed-eaters, rather than those with more gracile beaks, as in insectivores. Among the very few reported examples among the passerines, most have robust beaks (Table 1). Among the swallows with more gracile beaks, forced copulation attempts are usually of multiple males ganging up on a female.
- *Aggressive copulation is more common when females' movements are restricted.* Because captivity restricts females' opportunities for escape, SDT predicts aggressive copulation is more likely in captive than free-living birds.
- *Aggressive copulation is more common in species in which males defend and broker to females some resource limiting females' reproduction.* When resource needs (e.g., nesting cavities) constrain female movements, females should be more vulnerable to aggressive conditioning and aggressive copulation than when males are unable to broker female access to resources (Gowaty, 1996a, 1997). Thus, for example, all else equal, we predict that among cavity-nesting taxa there is more aggressive copulation than among closely related open-cup nesting taxa. Or, aggressive copulation is more frequent in populations of eastern bluebirds as a function of the availability of nesting cavities. When nesting cavities are rare, female vulnerability to aggressive copulation will be greater than when nesting cavities are abundant.
- *Aggressive copulation is more common when males are larger than females.*

When males can overwhelm females based on size alone, aggressive copulation should be more common than when males and females are more evenly matched or when females are larger than males. This is the basis for the prediction that among the Sulidae (gannets and boobies) aggressive copulation should be more common in the gannets, which are sexually size monomorphic, than in the boobies, in which females are larger than males. This reasoning also predicts levels of intraspecific, intra-pair aggressive courtship as a function of within-pair size dimorphism. Among the listed passerines in Table 1, almost all have males larger than females.

- *Aggressive copulation is more common among colonial than solitary species.* In colonial species in which son philopatry predominates (Greenwood, 1980), the presence of near neighbors may facilitate male kin coalitions and the development of social conventions (Wilson *et al.*, 1996; Smuts, 1992). In these species one expects more cases of grouped males ganging up on, chasing, and attacking females. SDT predicts that because grouped males may be able to collaborate to overcome female behavioral resistance, aggressive copulation will occur among colonially breeding species. Many more than half of the species listed in Table 1 are colonially or weakly colonially breeding species.

ULTIMATE EXPLANATIONS FOR FORCED COPULATION

The immediate fertilization enhancement hypothesis

The usual functional explanation for forced copulation in birds is that it increases the likelihood of immediate fertilization success for males with females who otherwise would not mate with them (Thornhill, 1980; Thornhill and Thornhill, 1983; Shields and Shields, 1983). McKinney *et al.* (1983) and others see forced copulation as a secondary reproductive tactic of male birds. An examination of the morphology and physiology of avian copulation renders this functional explanation for forced copulation suspect. Our

TABLE 1. *Non-anseriform avian species in which apparently forced and aggressive/resisted copulations have been reported.*

Species ^a	Free-living (F) or captive (C)	Female behavior	Male behavior	Size ^b Dimor.	Source
Procellariiformes					
Northern fulmar <i>Fulmarus glacialis</i> *	F	No description	No specific description	Y	Hunter <i>et al.</i> , 1992
Ciconiiformes					
White ibis <i>Eudocimus albus</i> **	F	"protest" and "lack cooperation"	may bite, beat female's head	Y	Frederick, 1987a, b
Charadriiformes					
Razorbill <i>Alca torda</i> *	F	do not allow access to cloaca and may eject unwanted sperm	repeated "aggressive" mounting	U	Wagner, 1991
Common murre <i>Uria aalge</i> *	F	attack aggressive males, stand upright to throw off males, or run away	multimale groups attack incoming females and pin them to the ground	N	Birkhead <i>et al.</i> , 1985
Atlantic puffin <i>Fratercula arctica</i> *	F	dive or swim away from male	attempt to mount females in the water	N	Creelman and Storey, 1991
Coraciiformes					
White-fronted bee-eater <i>Merops bullockoides</i> *	F	fly away; pressing, tail, cloaca to ground; perch in tree with tail spread, spend all time in nest hole during fertile period	multiple males chase, "subdue" females, 85% of chasing males were breeders; 13% helpers	N	Emlen and Wrege, 1986
Passeriformes					
Rook <i>Corvus frugilegus</i> *	F	females resist mounts by multi-male groups	multimale groups attempt to mount females	N	Roskaf, 1983
Red-winged blackbird <i>Agelaius phoeniceus</i>	F	retreat and fly away	chase and "pouncing on female"; may involve more than one male	Y	Westneat, 1992
Tree swallow <i>Tachycineta bicolor</i>	F	fly away from male	chased and trapped female in nestbox	N	Vernier <i>et al.</i> , 1993
Purple martin <i>Progne subis</i> *	F	no description of female resistance	no description of male aggressive behavior	N	Morton <i>et al.</i> , 1990
Sand martin <i>Riparia riparia</i> *	F	fly away from chasing males	chasing females	N	Jones, 1986
Barn swallow <i>Hirundo rustica</i> *	F	fly away	chase females	N	Møller, 1985, 1987 a, b
Cliff swallow <i>Hirundo pyrrhonota</i> *	F	flutter wings/struggle vigorously	alight on back and grasp female's nape with beak	N	Butler, 1982

TABLE 1. *Continued.*

Species ^a	Free-living (F) or captive (C)	Female behavior	Male behavior	Size ^b Dimor.	Source
Aquatic warbler <i>Acrocephalus paludicola</i>	C	no description	grip female by nape	N	Birkhead, 1993
House sparrow <i>Passer domesticus</i>	F	fly away	multi-male chase/display; grab neck feathers of female with beak	S	Møller, 1990
Indigo bunting <i>Passerina cyanea</i>	F	alarm calls and "resist"	chase; push to ground	N	Westneat, 1987
Northern oriole <i>Icterus galbula</i>	F	fly away	chase female	N	Edinger, 1988
Pied flycatcher <i>Ficedula hypoleuca</i>	F	fly away	chase females	N	Alatalo <i>et al.</i> , 1987; Bjorklund and Westmann, 1983
Zebra finch <i>Taeniopygia gutta</i> *	F & C	fly and hop away and peck at male	chase or pounce on female and hold head feathers	S	Birkhead <i>et al.</i> , 1989; Burley <i>et al.</i> , 1996a, b; Birkhead <i>et al.</i> , 1988a, b

^a Colonial and rookery breeding species designated by (*) and (**), respectively.

^b Information for size dimorphism taken from Dunning (1993); Y = dimorphic, N = not dimorphic, U = unknown, S = difference in average body weights, however, ranges overlap. Unless otherwise noted, males are larger than females when size dimorphism is present.

examination of the mechanics of copulation demonstrates how knowledge of the proximate mechanisms of a trait—in this case, aggressive copulation—informs evaluation of hypotheses of ultimate or functional causation.

Fitch and Schugart (1984) claimed that forced copulation is impossible in most birds because for sperm transfer to take place, females must evert their cloacae.

Since males of most avian species have no intromittent organs, the ductus deferens ejects sperm into the middle of the three compartments of the cloaca (Fig. 1). Males in most species of birds probably also have to evert their cloacae during so-called "cloacal kisses" of avian copulation to facilitate sperm transfer. Also, typical avian copulations are extremely rapid, often taking only seconds to complete. In

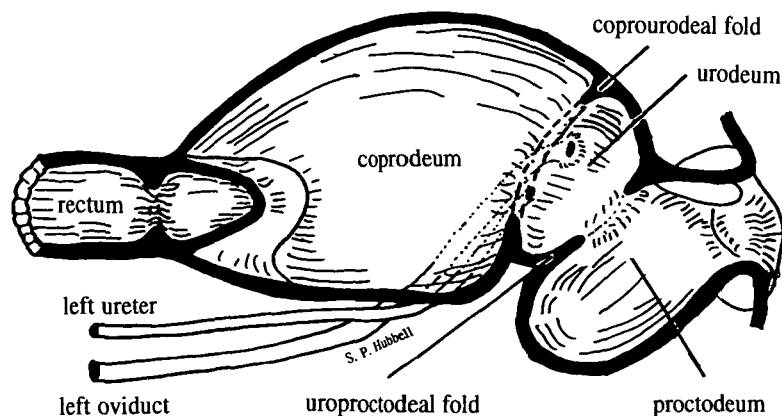


FIG. 1. A schematic drawing of a stylized avian cloaca.

the vast majority of bird species, *i.e.*, about 97 to 98%³ of species, females must actively participate in copulation for sperm transfer to take place; therefore, the likelihood that male birds successfully force inseminate seems small. An objection to this reasoning is that if the cost of not complying is high for females, males can force females to cooperate because of the risks to them from male aggression. This logic has some validity. We argue, however, that because sperm transfer occurs in the cloaca, forced insemination is unlikely to be successful in achieving fertilizations, because females have so many options for ridding themselves of unwanted inseminate. It is these options for successful post-insemination resistance that render the Immediate Fertilization Hypothesis for forced copulation in birds truly suspect. Consider just a few of the most obvious design features of females' cloacae.

The cloacae of birds: Built-in female resistance mechanisms

The cloaca (Fig. 1) is a common chamber through which pass the products of the digestive, reproductive, and urinary systems (Hyman, 1942). It opens to the outside through the vent. Though folds and compartmentalizations across bird species are variable (King, 1981), two internal mucosal folds typically divide the cloacae into three parts. The coprodeum is next to the rectum; in some descriptions it is simply the caudal end of the rectum, and a coprourodeal fold and valve may or may not separate the two sections (Jacobshagen, 1937). The urodeum, the second chamber, is the shortest section of the cloaca; the uroproctodeal fold separates it from the proctodeum. The proctodeum; which is wider than the urodeum and thereby easily identified, is the third chamber and empties through the vent.

The coprodeum receives the feces from the end of the digestive tract. In some bird

species the feces travel through the urodeum to the proctodeum to the vent. In others, the coprodeum can be everted through the membranous folds directly through the vent. From the perspective of SDT, basic descriptions of the internal coprodeum are intriguing:

“... The internal mucosal junction with the rectum is unmarked except (a) in the Ostrich (and possibly some other ratites) in which there consistently appears to be a true rectocoprodeal fold and (b) in Anatidae in which there is an abrupt and conspicuous ridgelike change in the gross appearance of the mucous membrane caused by a sudden transition to a stratified squamous epithelium in the coprodeum. However, in most birds the boundary between the rectum and coprodeum is indicated only by an expansion in the calibre at the beginning of the coprodeum. In the domestic fowl the mucosa is lined by villi which are similar to those of the rectum, apart from being somewhat lower and broader. Crypts and simple glands are present. The epithelium is tall columnar with goblet cells. Similar villi occur in some passerines (*e.g.*, the Zebra Finch and Singing Honeyeater); in the Emu the surface area of the coprodeum is further increased by folds which carry villi” (King and McLelland, 1984, p. 189).

Remember that columnar epithelium is absorptive and digestive as are the villi (Curtis and Barnes, 1989) that increase the surface area usually of the intestine, but in this case the cloaca. Furthermore, goblet cells secrete mucus (Curtis and Barnes, 1989) that lubricates the feces and protects the surface of the intestine from proteolytic enzymes, a fact that suggests that the proctodeum too might require protection from its own digestive secretions.

The urodeum receives urine from the ureters and, in males, the sperm from the ductus deferens. In females, the left oviduct opens into the urodeum, as well. King and McLelland (1984) note (p. 191) that in some species irregular furrows and folds invest the mucosal epithelium of the uro-

³ There are 7 species of ratites, 46 species of tinamous, and about 150 species of ducks and geese. Thus out of a world total of about 9,000 extant birds, those species with intromittent organs represent about 2–3%. See also Briskie and Montgomerie (1997).

deum; in some the epithelium is tall columnar with secretory goblet cells; in some species crypts and glands are present. Sometimes, the epithelium is stratified squamous, rather than columnar, and in others there is a mixture of epithelia. In waterfowl females, a membrane that is not absorbed until sexual maturity (probably under the action of estrogen) at the beginning of the first breeding season covers the opening of the oviduct.

The mucosa of the proctodeum is usually stratified squamous epithelium, though notably in the waterfowl it is simple columnar, suggesting that the absorption of water and other liquids can take place in the proctodeum. The mucosa of the proctodeum contains the globular cloacal bursa in which immunologically competent B lymphocytes differentiate. This bursa involutes in most bird species at sexual maturity; however, in ratites it retains its full size for life (King and McLelland, 1984). In some species, a dorsal proctodeal gland occurs in males. In chickens and other domestic fowl mucous glands invaded by lymphoid tissue comprise the proctodeal gland. In domestic quail this gland has numerous openings and secretes a white frothy fluid, transferred to the oviduct during copulation. In many species in both sexes lateral proctodeal glands also occur, although their functions remain apparently undescribed (King and McLellan, 1984). The intromittent phallus of waterfowl and the ratites is in the proctodeum.

When copulation takes place in the majority of bird species, female and male urodea, the middle chamber of the cloacae, come into contact. A male deposits sperm directly into a female's urodeum unless a phallus delivers sperm nearer to the opening of the oviduct. Some birds, like the galliforms, have a nonintromittent phallus, which delivers sperm more closely to the opening of the oviduct while the females' urodeum is everted making contact with the air; this nonintromittent phallus acts a bit like a slide directing the course and flow of the sperm to the surface of the everted urodeum. In those species without any phallus, the male and female urodea "kiss" during sperm transfer.

The details of the anatomy of copulatory machinery suggest that female birds have several potential pre-existing means for resisting, or even avoiding altogether, forced insemination. If males force females to copulate, *i.e.*, if passerine males can force females to evert their cloacae, it would seem unless the ductus deferens contacts the oviductal opening, females could use the powerful cloacal muscles, presumably originally evolved to evacuate waste products, to cleanse themselves of unwanted inseminate. In most birds there are five striated muscles surrounding the cloaca and vent: transverse anialis; sphincter ani; contractor cloacalis; suspensor ani; and dilator ani (Nishi, 1938). When birds produce urine, they evacuate it into the bowl of the urodeum where powerful muscular contractions suck it into the coprodeum—back towards the rectum. Thus, the muscular coprodeum everts urine and feces through the urodeum and the proctodeum. This is interesting because of the existence of powerful muscles that expel the contents of the urodeum. Selection could act easily on females to use these powerful muscles to rid themselves of unwanted inseminates. An example may be in Nelson (1978) which has a photograph of a northern gannet female evacuating her cloaca during a forced copulation! In addition, digestive enzymes could denature any material sucked back into the coprodeum. In some species retroperistaltic waves originating in the coprodeum and terminating in the intestines move urine from the middle chamber of the cloaca into the intestine (Farner, *et al.*, 1972). Might females not use similar retroperistaltic waves to place sperm in an ultimately hostile environment of the intestine? The curious glands of undescribed function in the proctodeum may also secrete substances that females may use to differentially affect the success of sperm from preferred and aggressive copulations.

One point of our discussion of cloacal anatomy is that even if males of a species without an intromittent organ forcefully inseminated a female, she has built-in counter-mechanisms that she may use to de-

crease the likelihood that forced inseminations result in fertilization. Our conjecture emphasizes that more research on the anatomy and physiology of the cloaca is necessary and promising. A second point is that the cloacae of females and males of the same species may function somewhat differently. In this light it is especially interesting that modern avian anatomists, physiologists, and behavioral ecologists know almost nothing about the cloaca of females. As long as we thought the function of the cloaca and surrounding musculature were simply to evacuate waste products and eggs, this knowledge deficit was tolerable. We hope that this knowledge deficit is no longer reasonable and tolerable. A third point is that new research should focus, not on flaccid, dead cloacae and surrounding musculature, but on physiologically active, alive materials (D. Homberger, personal communication).

The seldom-attended-to facts of cloacal anatomy and physiology have made us wonder if the Immediate Fertilization Enhancement Hypothesis is an adequate explanation for why males attempt forced copulations in passerines and other species lacking intromittent organs. Might other explanations be more consistent with the known behavioral, physiological, and morphological variation in such birds? These seldom-attended-to facts and the logic of SDT stimulated the prediction that compared to waterfowl, most passerines will have fewer post-insemination resistance mechanisms past the cloaca. So, for example, it does seem logical that female passerines behaviorally control copulations just as several authors have recently proclaimed (Stutchbury and Neudorf, 1997), both because of the mechanics of passerine copulation and because the cloaca provides so many opportunities for expelling or denaturing unwanted sperm. Thus, if those who claim female passerines "control" copulation are correct, sperm management organs to kill or inhibit fertilization would seem redundant; thus, SDT predicts for species in which females do control copulation that sperm management organs are true sperm storage organs, that occur only in those

species in which females seek copulations with more than one male.⁴

Built in counter-mechanisms also seem available to female waterfowl, in which males have true intromittent organs. During copulation in ducks and geese, females do not have to even their urodea in order for sperm to contact the oviduct. Rather, males can inseminate females without females' cooperation. Unlike the mammalian penis, sperm travels on the outside of the grooves of the anseriform penis, not through an internal canal (Hyman, 1942). And, in order for the phallus to contact the opening of the oviduct, the phallus must go through the proctodeum into the urodeum. Therefore, the struggling involved in some duck copulations may be useful to females if it dislodges sperm from its path to the oviduct. The modified mucosa of the urodeum and coprodeum of waterfowl would seem to allow absorption of fluid including sperm. As in other birds, the cloacae of female anseriforms have powerful striated muscles for evacuating their contents. After forced insemination, females should be able to evacuate their cloacae, just as happens in other

⁴ Data which came to our attention after we formulated these ideas include studies on captive zebra finches (Burley *et al.*, 1996a,b). Apparently forced extra-pair copulations occurred frequently—80% of all extra-pair copulations were aggressive. When fertile females were subjected to aggressive extra-pair copulations, forced extra-pair copulations had no effect or a negative effect on the rates of putative paternal exclusions, meaning that forced extra-pair copulations never resulted in offspring. Yet, 28% of chicks were from unforced extra-pair matings, which means that unforced extra-pair copulations were highly effective in producing offspring. Therefore, zebra finch females must be able to differentially allocate eggs to certain males' sperm, or they are able to evacuate sperm from forced copulations from their cloacae, or able to trap and/or disarm sperm of nonpreferred males or able to selectively use stored sperm. This is an important study because it is the first able to examine the effect of aggressive copulation on fertilization success. The results suggest that aggressive copulation does not increase the fertilization success of male zebra finches. It confirms among other things (Burley *et al.*, 1996) that female zebra finches are in control of fertilization. We mention it because of the interesting juxtaposition between very high rates of aggressive copulation with little or no likelihood of increased fertilization success, a clear empirical suggestion that some other functional explanation is needed to explain aggressive copulation in this and perhaps other species, as well.

species without intromittent organs. One other modification of waterfowl cloacae seems a female resistance mechanism. The oviduct has a membranous cover until females are sexually mature and often up to the time they are a year and a half old. This membrane may prevent fertilization after forced insemination of younger birds.

Besides these already observed traits in waterfowl, other post-insemination resistance mechanisms may also exist. SDT predicts that if sperm successfully enter the oviduct of females, management tissues designed to kill or inhibit sperm movement may operate. In other words, if immediate fertilization enhancement is the functional explanation for aggressive copulation, selection should act on females to favor sperm management tissues that do not nourish or store sperm. Thus, in contrast to the prediction about passerine sperm management tissues, waterfowl are more likely to have sperm management tissues that kill or inhibit the efficacy of sperm. Could this be one of the functions of the lateral proctodeal glands? The Sexual Dialectics Hypothesis also predicts that females may ovulate facultatively. It predicts that females might use rapid and repeated matings with preferred males to facilitate sperm swamping (Birkhead and Møller, 1992). If matings with preferred males are female tactics, females should solicit them enthusiastically.

Thus, altogether it seems unlikely that forced inseminations would often be successful at fertilization in any birds. Successful fertilization after forced insemination should be especially unlikely in passerines, and pretty unlikely in anseriforms too. We expect that the relatively large number of reports of aggressive copulation in birds is a by-product of the large number of studies on avian social and reproductive behavior, rather than a characteristic of the Aves. Consistent with our expectation, the number of published reports in birds remains relatively small in comparison to the large number of studies on avian reproductive behavior. Our most important point, however, is that after this brief review of the anatomy and physiology of avian copulation, we hope readers will at least entertain the possibility that other functional expla-

nations of forced copulations in birds besides the Immediate Fertilization Enhancement Hypothesis are worth considering and perhaps testing.⁵

"Punishment" may be an alternative explanation for aggressive copulation

Another explanation for forced copulation is that attempts by males to aggressively copulate condition female behavior for male(s) advantages either immediately or for the future. Aggressive conditioning means that some aversive stimuli condition individual behavior negatively (Clutton-Brock and Parker, 1995). In this case one individual modifies another's behavior for their own advantage. Punishment may decrease the likelihood that females will exhibit some behavior normally disadvantageous to the male(s) at the time males are aggressive to her or, if she can remember, in the future. Thus, an alternative explanation emphasizes not "copulation" but "aggressive" in the term, "aggressive copulation." This idea suggests that it is possible that some observations of aggressive "copulation" were just as likely to be male aggression against females rather than copulation attempts. This logic led us to wonder: How often have others mistakenly interpreted male aggression against females as "copulation"?

THE CODE HYPOTHESIS

Aggressive copulation conditions female behavior for male advantage

Heinroth (1911) was the first to theorize that consortships in mallards and other ducks arose despite the lack of male parental care because females have "the advantage of living with a mate" who defends

⁵ Note that the existence of basic morphology and physiology facilitating post-insemination ridding of sperm by females do not depend on the existence of forced or coerced copulation. Most seem to be by-products of having a common receptacle for products of reproductive, digestive, and urinary tracts.

her against “dangerous” nearby solicitors.⁶ Recently, Mesnick (1997) reviewed reproductive behavior in a wide variety of species and hypothesized that females choose mates for protection from other males. Certainly, Mesnick’s resurrection of Heinroth’s (1911) idea and her restatement of Brownmiller (1975) as an hypothesis is worthy of empirical attention.

Given the possibility then that females need “bodyguards” because of the threat of aggressive copulation, and given our suspicion that much aggressive “copulation” is really about attempts by males to aggressively condition female behavior for their own or others’ advantage, the question becomes: for what advantage, if not for immediate fertilization enhancement?

Male aggression against females can benefit aggressive males in a number of ways (Smuts, 1992; Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995). For example, it can increase the likelihood that males who might not have any mating success in what would otherwise be a socially polygynous or promiscuous system will enjoy reproductive success benefits via social monogamy. When the environment is dangerous for females, “protective males” (Heinroth, 1911) may benefit from increased paternity certainty. This may be because males may require females to “trade” copulations for protection. The creation of a dangerous environment for females and the subsequent requirement for

protection from males may facilitate the evolution of social monogamy even in species with precocial young. The difference between what Heinroth (1911) said and what we are saying is just that males may themselves create the dangerous environment for the advantages they will accrue. This scenario would be advantageous for some males in a population, especially those who might otherwise have little or no opportunity to mate. Thus, we see the (unconscious) coalition among males originating among those that would have low reproductive success in socially polygynous or promiscuous mating systems. So, we expect that the protection for paternity scheme disadvantages some males: namely, those males who would otherwise have high reproductive success under social polygyny or promiscuity. We suspect that such males are those from whom females enthusiastically solicit copulations. Thus, we differ from Brownmiller’s (1975) original expectation in that we do not predict that all males benefit from a system of protection for paternity. Below (Fig. 3) we show how variation in female vulnerability to male aggression may affect the reproductive success of males that would potentially have low fitness under less coercive mating systems.

Fitness advantages of male aggression against females

Figure 2 shows how a system of male aggression against females can evolve so that fitness benefits accrue to males. Keep in mind that social monogamy via trades of genetic paternity for protection may be a disadvantage for those males who would be able to mate with more than one female in social polygyny or with many females in a system of social promiscuity. Therefore, Figure 2 describes the fitness pathways for aggressive males and their “beneficiaries,” those who might otherwise have very low or no reproductive success at all under social polygyny or social promiscuity. Some (Smuts, 1995; Gowaty, 1997) posit that this advantage of male aggression against females favors the evolution of male coalitions or the emergence of social conventions (Wilson *et al.*, 1996), a way of thinking about male aggression against females

⁶ This is not unlike the hypothesis of Brownmiller (1975) to explain the prevalence of rape and social monogamy in humans. She wrote, “. . . Female fear of an open season of rape, and not a natural inclination toward monogamy, motherhood or love, was probably the single causative factor in the original subjugation of woman by man, the most important key to her historic dependence, her domestication by productive mating” (p. 16). Although many other factors are likely to be associated with social monogamy in people, Brownmiller’s (1975) ideas stressed that many men benefit when even just a few men rape. This admittedly controversial idea pivots on the assumption that because one woman is raped, other women will fear that they too could be raped, and therefore, either consciously or unconsciously modify their behavior in ways that decrease the likelihood that they will be raped. This idea has recently been given some force as an explanation for many nonhuman animal consort patterns in the form of the Body Guard Hypothesis (Mesnick, 1997).

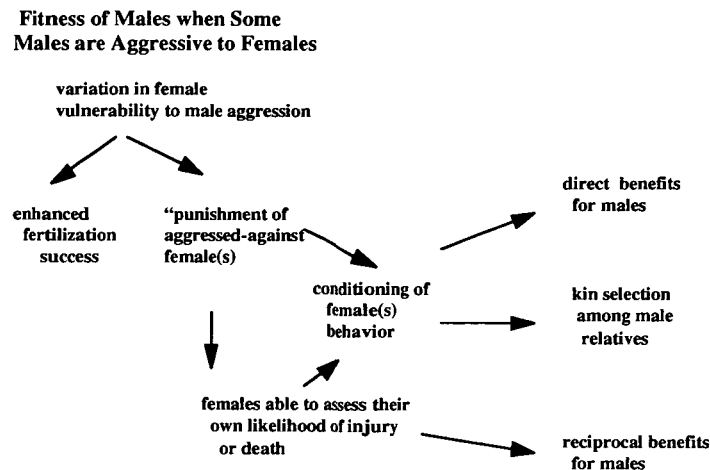


FIG. 2. Steps by which the creation by some males of a dangerous environment for females leads to fitness benefits for many or most males.

that has the advantage of not requiring conscious conspiracies among males.

A game theoretical analysis would pit males with high fitness expectations under social polygyny or promiscuity against those males with low fitness expectations under social polygyny or promiscuity. Assume that forced insemination is impossible. Call those males with high fitness expectations "P males"; call those with low fitness probabilities "Z males." One problem to be solved is under what conditions would aggression against females of one or a few males benefit Z in comparison to P males. Another is what conditions favor the expression of aggression against females by one Z male rather than another? The solution to the first problem is trivial: selection may result in aggression if it increases the Z males' fitness. This is classic individual advantage (Fig. 2). Under kin selection, selection will favor aggression against females when kin fitness benefits minus the costs to the aggressor are greater than his fitness payoffs under social polygyny or promiscuity. Under reciprocal benefits, the fitness payoff to a lone aggressor seems less likely to result in a positive function compared to other Z males; however, the fitness payoff to males in groups that aggress against females seems more likely to yield positive payoffs for all the males in such a group. Under a reciprocal benefit policy,

both the costs and the benefits for Z should be equalized. These relationships are schematically noted in Figure 2.

For Figure 2 assume for simplicity that forced insemination is impossible. Fitness advantages for aggressive males accrue only from the conditioning of the behavior of the aggressed-against females. If females are even occasionally vulnerable to male aggression when behaving in some predictable ways (*e.g.*, moving around alone or unaccompanied by other males), and if other females can assess their own likelihood of injury or death if they behave in ways similar to aggressed against females (perhaps because they see the aggression of males towards other females), the condition exists for benefits to accrue for other males in the population besides the aggressive males. These fitness benefits for nonaggressive males may arise through direct effects, kin selection (brothers or other kin are aggressive to relatives' mates), or reciprocal altruism (Trivers, 1971), though it would seem easiest to evolve under a system of kin selected advantage to males.

Note that if one relaxes the assumption that forced fertilization is impossible, any small advantage associated with enhanced fertilization success could amplify the selective force of aggression via individual selection. This in turn would favor trades of protection for genetic paternity for other

males and set in motion individual dynamics associated with reciprocal altruism.

The above scenario will work if there are only a few aggressive males in the population and if females can modify their behavior after observing aggression against other females. It will work if all or some males are facultatively aggressive against some females. Once fitness benefits for nonaggressive males arise, conditions are in place for the evolution even within the same male of facultatively expressed aggression against and protection of females. Thus, males may create an environment in which it pays females to "buy" protection from them. This is the Creation of a Dangerous Environment (CODE) Hypothesis for the evolution of aggressive "copulation" (Fig. 3).

THE CODE HYPOTHESIS FAVORS SOCIAL MONOGAMY

The CODE hypothesis, like the Immediate Fertilization Enhancement Hypothesis, is testable. The CODE hypothesis is a variant of the Constrained Female Hypothesis (Gowaty, 1996a) that theoretically explains the distribution among females of extra-pair paternity in socially monogamous passerines. The Constrained Female Hypothesis says that males exploit variation among females for their own advantages, thereby manipulating female mating behavior. Social monogamy through "trades" of fertilizations for protection is a type of mating system in which males manipulate females' reproductive options through brokering resources to females; in this case, the resource of interest is protection.

The CODE Hypothesis for aggression against females theoretically explains the maintenance of "forced copulation" in species in which successful forced insemination is unlikely or impossible. The CODE hypothesis for social monogamy provides an answer to the question of why females that have less costly means of resisting forced insemination put themselves at further risk of injury and death by continuing to behaviorally resist. The CODE Hypothesis says that even if females do not resist the "forced copulation" attempts, that the point for males is to provide enough aver-

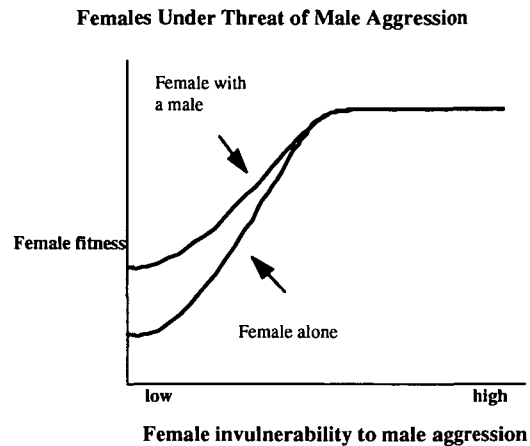


FIG. 3. A graphical expression (Gowaty, 1996a) of the Constrained Female Hypothesis for the evolution of social monogamy via "trades" of fertilizations for protection that is associated with the creation by males of a dangerous environment for females. The horizontal axis represents combinations of intrinsic variation in females and their environments that increase or decrease females' vulnerabilities to male aggression against them. For some combinations of females and environments represented on the left-hand side of the graph, female fitness is enhanced by the protection of a consort male, a situation that favors the evolution of social monogamy. For other combinations of females and environments represented on the right-hand side of the graph, female fitness is not enhanced by the protection of a pair male, a situation that provides no obvious selection pressure for social monogamy.

sive stimuli to modify female behavior. The CODE Hypothesis for aggressive copulation favoring social monogamy suggests that females may continue to resist because they are fighting for their lives and not just to avoid insemination.

Figure 3 illustrates an aspect of the Constrained Female Hypothesis (Gowaty, 1996a) and some potential dynamics of social monogamy through "trades" for protection from the perspective of females. On the graph female fitness is a function of a combination of females' intrinsic abilities to avoid or resist male aggression and environmental qualities that increase or decrease females' vulnerabilities to male aggression against them (*e.g.*, females larger than males; habitats with hiding places, etc.). The upper curve represents females' fitness when they are with consort males; the lower curve when they are not with consort males. The curves are congruent on

the right side of the graph to represent environmental heterogeneity or variation among females' characteristics such that some females' fitnesses are unaffected by the presence of a male consort. The model says that some females are more vulnerable to males than others. This model predicts females on the left hand side of the graph experience more social constraint than females on the right. Because they are more vulnerable to male aggression, they are unlikely to willingly copulate with preferred extra-pair males than females to the right. This graph demonstrates conditions leading to variation among females in extra-pair paternity by preferred sires in organisms such as ducks in which male contribution to offspring care is negligible or nonexistent. The creation of a dangerous environment for females might be an especially effective strategy in those species in which females are able to raise their offspring without any help from males and in which males cannot monopolize feeding resources, so that males cannot use resource brokering as a mechanism for manipulating female mating behavior (Gowaty, 1996a, 1997).

Predictions of the CODE and immediate fertilization enhancement hypotheses

Predictions of the CODE hypothesis for social monogamy include:

- Aggressive "copulation" is directed at both fertile and nonfertile females, in waterfowl, particularly during nonbreeding seasons before the time when females are fertile.
- Males direct aggressive "copulations" at unmated or unguarded females or females moving unescorted in the environment, often in view of other females.
- Aggressive copulation correlates with modifications of female behavior in such a way to favor socially monogamous consorts, even without paternal care.
- Fertilization success from aggressive copulation may be absent or very low.
- Paired as well as unpaired males attempt to aggressively copulate with females besides their social mates.
- The behavior of females, including nonaggressed against females, varies before

and after aggressive "copulation" attempts in such a way that opportunities for females to extra-pair copulate with preferred males declines.

- Females' vulnerabilities to male aggression against them varies, so that smaller females or females nesting in more open habitat have increased vulnerability to male aggression with the removal of their social consorts.
- Female behavior, such as their paths during foraging, is altered by the removal of aggressive males in an area.
- When males are aggressive to only one or a few females in naive populations, the behavior of many females changes.
- The behavior of females not aggressed against is modified similarly to females that are aggressed against.
- A nonintuitive prediction of the CODE hypothesis is extra-pair paternity will be higher for females with the least, not the most vulnerability to aggressive copulation. For example, larger females or those females nesting in less open habitat will have more extra-pair paternity from preferred mates than smaller females or females nesting in more open habitat. This follows from a consideration of SDT (Gowaty, 1997) that assumes that selection may favor females with superior offspring viabilities when they share their gametes with preferred extra-pair partners.
- Variance in reproductive success among males is highest for males who socially consort with females least vulnerable to male aggression.

In comparison, the Immediate Fertilization Enhancement Hypothesis makes the following contrasting predictions to the CODE Hypothesis.

- Aggressive copulation attempts are on fertilizable females only (because of the potential risks to males of their own injuries in aggressive interactions).
- Fertilization success from aggressive copulation is as frequent as from copulations with preferred partners in which females do not resist.
- Extra-pair paternity is highest for females most vulnerable to aggressive copulation.

- Variance in reproductive success among males is highest for males who socially consort with females most vulnerable to aggressive copulation.
- Notably, it makes no predictions about modifications of female behavior for males' advantages.

Evaluating predictions

No one we know about has evaluated predictions of these hypotheses for any bird species. However, even though it appears that observation agrees with prediction at their grossest (e.g., comparisons between waterfowl and perching birds), it seems to us unfair to claim a test of these ideas with already collected data or reviews from the literature, because of the danger that these ideas came from our familiarity with existing data. We don't think this is what we did, but it remains a possibility. We hope, therefore, that this paper will stimulate future empirical studies.

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