

Research

The limits of sexual conflict in the narrow sense: new insights from waterfowl biology

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Sexual conflict occurs when the evolutionary interests of the sexes differ and it broadly applies to decisions over mating, fertilization and parental investment. Recently, a narrower view of sexual conflict has emerged in which direct selection on females to avoid male-imposed costs during mating is considered the distinguishing feature of conflict, while indirect selection is considered negligible. In this view, intersexual selection via sensory bias is seen as the most relevant mechanism by which male traits that harm females evolve, with antagonistic coevolution between female preferences and male manipulation following. Under this narrower framework, female preference and resistance have been synonymized because both result in a mating bias, and similarly male display and coercion are not distinguished. Our recent work on genital evolution in waterfowl has highlighted problems with this approach. In waterfowl, preference and resistance are distinct components of female phenotype, and display and coercion are independent male strategies. Female preference for male displays result in mate choice, while forced copulations by unpreferred males result in resistance to prevent these males from achieving matings and fertilizations. Genital elaborations in female waterfowl appear to function in reinforcing female preference to maintain the indirect benefits of choice rather than to reduce the direct costs of coercive mating. We propose a return to a broader view of conflict where indirect selection and intrasexual selection are considered important in the evolution of conflict.

Keywords: forced extra-pair copulations; genital evolution; sexually antagonistic coevolution; female preference; ducks

1. INTRODUCTION

Parker [1] formally proposed the concept of sexual conflict to describe the clashing evolutionary forces created by the divergent interests of individuals of different sexes. This original broad definition encompasses a wide range of potential conflicts over mating, fertilization, reproductive investment and parental care [1]. The evolutionary consequences of conflict can theoretically include a broad range of outcomes such as speciation [2,3], extinction [4], latent conflict without observable effects [5] and in some circumstances in a dynamic coevolutionary arms race between the sexes, called sexually antagonistic coevolution (SAC) [4,6–8]. When SAC occurs, derived character states that further the sexual interests of one sex select for derived character states in the other sex that increase their capacity to manage the conflict.

As the theoretical framework of sexual conflict develops, a narrower sense view of sexual conflict has been proposed to distinguish it from traditional sexual selection. We refer to sexual conflict in the narrow sense as the view that selection acts on females

only to reduce the direct costs of mating interactions with males (costs paid by the female in either viability, fecundity or offspring survival). Narrow sense sexual conflict explicitly excludes indirect costs to females (paid via her offspring in either reduced attractiveness or mating success) as being relatively unimportant in the context of conflict [4,6,9–12]. Further, under this process, the viability cost of mating preference leads to the evolution of female narrower preference or a higher preference threshold [4,10,11]. Broad sense sexual conflict, on the other hand, includes conflict over both mating and fertilization [8]; so by necessity, it includes direct and indirect selection on mating preferences. We advocate a broad view of conflict where intrasexual selection is at least as important as intersexual selection in explaining the origin of harmful male traits, and where female preference and resistance and male display and coercion are considered independent. We find that while many papers acknowledge the broader intellectual origin of the concept of sexual conflict, many have focused exclusively on sexual conflict in the narrow sense [4,6,9–12].

A large majority of influential studies [4,9–11,13] of conflict have emphasized conflict over mating rate and how it leads to more stringent female preferences following the intersexual framework developed by Holland & Rice [14]. Over the same period, the role

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of male–male competition in the evolution of traits that allow males to manipulate and coerce females have received comparatively little attention, although recently some studies have begun to address its importance [15,16]. Modelling sexual conflict in terms of female mating rate began with Rice & Holland [17], who presented it as an example of interlocus evolutionary conflict. Holland & Rice [14] then proposed a verbal ‘chase-away’ sexual selection model in which a new male secondary sexual trait evolves in response to a pre-existing female sensory bias; the male trait is so stimulating that females mate at a higher frequency than is hypothesized to be optimal for their own fitness. Because choosy females that mate less frequently will have greater fitness, natural selection to lower mating rate will raise the sensory threshold necessary to elicit the bias. The higher threshold of sensory bias will in turn select for exaggeration of the display trait, resulting in an escalating arms race that will be checked only by natural selection when costs of escalation are sufficiently high [14]. Gavrillets *et al.* [9] provided the first genetic model of SAC over mating rate, capturing the essence of Holland & Rice’s verbal model. This model concluded that female fitness derived exclusively from mating rate and that the inclusion of indirect benefits derived from her partner’s identity (see appendix in [9]) had no effect on female resistance or male manipulation. Many mathematical models have examined sexual conflict exclusively in terms of mating rate or other direct female costs [3,9,18–22], and many empirical studies have reflected this tendency [23–25].

In this paper, we have three aims. First, we review the limitations of the narrow sense view of sexual conflict. Second, we review the advantages of a broader sexual conflict framework. Third, we apply the broad framework to our study system of sexual conflict and genital coevolution in waterfowl.

In §2, we maintain that narrow sense models of sexual conflict have several problematic features that limit their applicability to many examples of sexual conflict in which females exhibit both distinct preferences for male displays and resistance to sexual coercion. These problems include: (i) failure to distinguish female preference and resistance; (ii) failure to distinguish male display and coercion; (iii) over-emphasis of chase-away as an explanation for the evolution of male traits that negatively affect female fitness; and (iv) the exclusion of indirect effects as being unimportant in sexual conflict.

In §3, we support a broad view of sexual conflict where: (i) the importance of intrasexual selection is recognized; (ii) female preferences, resistance and male coercion display are considered independent phenotypic characters; and (iii) indirect effects become an integral part of sexual conflict.

In §4, we discuss how our recent research on genital evolution in waterfowl suggests that exclusion of indirect effects as important drivers or sexual conflict is problematic. In previous work, we have described the coevolution of male and female genitalia in waterfowl [26]. In waterfowl species that have evolved more elaborate phalluses, females have coevolved complex oviducts—i.e. blind pouches, and counter-sense

spirals—that appear to function to selectively exclude the phallus [27]. Coevolutionary elaboration is positively associated with rate of forced extra-pair copulations (FEPCs) [26]. Because female genital adaptations in waterfowl do not decrease the direct costs of male sexual coercion but appear to function solely in manipulating fertilization success ([27], and discussion in §4), these structures could not have evolved by a narrow sense sexual conflict mechanism that excludes indirect effects. In addition, in waterfowl, females choose a mate and form a pair bond over a period of weeks prior to the breeding season when sexual coercion is non-existent [28]. Females also resist mating with coercive males that subvert them by force during the breeding season [29]. Female preference and resistance in waterfowl are completely distinct, independent behaviours. However, narrow approaches in some sexual conflict literature define preference and resistance as being equivalent (§2*a*).

Previous authors have raised some of these issues discussed here [5,7,8,10,30–35] but we further expand and unify some of these views. We do not discuss conflict over parental care, or ‘intra-locus’ conflict that occurs when the optimum value for the same loci differs between the sexes.

2. PROBLEMS WITH SEXUAL CONFLICT IN THE NARROW SENSE

(a) *Preference and resistance synonymized*

Most narrow sense models of sexual conflict define all mechanisms that contribute to mating biases as forms of ‘mate preference’, including those that involve physical resistance and overt struggle [4,9,13,34,36]. Gavrillets *et al.* [9, p. 535] assert that ‘female preference’ and ‘female resistance’: ‘...are clearly identical in that they both describe situations where there are biases in the probabilities that females mate with different kinds of males, and both result in sexual selection by female mate choice among males’. Kokko *et al.* [34, p. 653] state that both preference and resistance are terms for female mating biases that, when expressed, generate a higher mating success for a subset of males, and further that the terms are logically interchangeable as both refer to the effort that females make to screen potential mates. Rowe *et al.* [20] viewed resistance as equivalent to preference because both bias the mating success of males, and explicitly defined preference as the probability distribution of mating. Arnqvist & Rowe [4, p. 79] state that resistance will reduce mating rate and result in a mating bias towards males that can bypass the resistance, which, they write, is by definition sexual selection by female mate choice. They define preference explicitly as any female trait that biases male mating/fertilization success [4, p. 17], and by such a definition, resistance would be a form of preference. More recently, Brooks & Griffith [37, p. 423] wrote: ‘Clearly female resistance to mating is well within the definition of mate choice, and like others [9,10], we see no point in distinguishing the mating bias that resistance causes to favour seductive or coercive males from the more conventional types of choice’. Although statements of the equivalence of resistance and choice sometimes include careful

caveats, these caveats do not specify or even allow for any conditions under which it is necessary to distinguish between resistance and choice, because the two will be considered the same every time they result in a mating bias.

It is true that both resistance to physical coercion and mating preference will create biases in male mating success [34], and that both will therefore result in sexual selection. However, the statement that both resistance and choice result in sexual selection *by female choice* excludes consideration of mating biases that result in sexual selection via male–male competition and have little or nothing to do with intersexual selection and female choice. By equating choice with resistance, the evolutionary origins, dynamics and consequences of female mating behaviour are obscured. Mating biases have been used as a modelling tool that allowed workers to concentrate on the outcome of sexual interactions rather than, to quote one reviewer, in the ‘often unknowable details of the selective forces acting on females, or the mechanisms that lead to that bias’ [34,38,39]. Although this may have been an understandable temporary measure, it has become a real problem for the field. To remain blind to the distinctions between these processes is misguided and unproductive, because the details will remain unknowable unless we recognize preference and resistance as biologically distinct phenomena, and develop testable predictions accordingly. A review on the current state of research on mate choice concluded that distinguishing the underlying mechanisms generating biases in mating success is of fundamental importance, and such mechanisms include active mate choice, passive attraction and male–male competition [40]. Biases in male mating success can arise by biologically distinct and potentially independent behavioural, physiological and anatomical mechanisms: (i) mating preferences that lead to active or passive mate choice and/or the establishment of a pair bond; and (ii) aversion or resistance to forced or coercive copulation and fertilization that result from male–male competition.

An obvious consequence of the narrow sense equivalence of resistance and preference is that autonomous mate choice and forced copulation—including rape in humans—are all considered forms of female choice. One has to consider only the difference between mate choice and rape in human sexual behaviour to recognize immediately that preference and resistance are not ‘identical’. Arnqvist & Rowe’s statement [4, p. 35] that: ‘male traits that decrease female fitness spread and are exaggerated because females ‘prefer’ them [i.e. bias mating or fertilization success towards males with more exaggerated or manipulative traits]’, ignores the fact that females may acquiesce to coercion to prevent males from hurting them or may be overpowered by the superior strength of males.

In many organisms, it is clear that behavioural or physiological preferences coexist in the same individuals with independent resistance mechanisms. Thus, preference or resistance may be elicited at different times by *the same male* in response to the different male reproductive strategies of trait display and physical coercion [41]. Preference and resistance are not

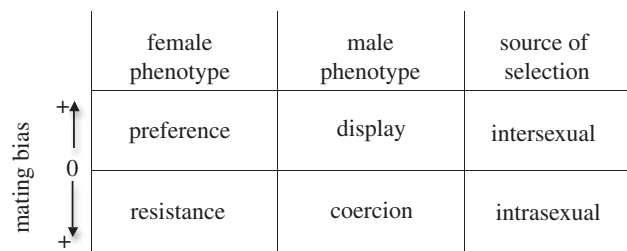


Figure 1. Mating biases originate by two different mechanisms. Female mating preferences select on male display traits through intersexual selection (top row). Male coercion evolves through intrasexual selection and selects for the evolution of female resistance (bottom row). Either intersexual mate preferences or intrasexual competition through male sexual coercion can result in mating biases (left arrows). Neither female preference and resistance nor male display and coercion are synonymous.

‘two sides of the same coin’ [10]. Rather they can have independent mechanisms of sexual selection (intersexual via female choice and intrasexual via male–male competition) acting upon each of them (figure 1).

Perversely, narrow-sense sexual conflict logic results in ‘preference’ models in which the mate identity is immaterial [9,20]. By redefining resistance as a form of preference, the very meaning of ‘mating preference’ has come unhinged from any logical meaning of the word.

Halliday’s definition [42, p. 4] of mate choice—‘Mate choice can be operationally defined as any pattern of behaviour, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than with others’—has been widely accepted in the field, but similar to mating biases it excludes any reference to process. Further, Halliday [42] stated that for the purpose of understanding the dynamics of mating systems, the precise selective mechanisms operating on female preference are irrelevant. We suggest that a mating preference is properly defined as a behavioural response to a potentially attractive sensory *stimulus* provided by a potential mate which affects the probability of mating. The fulfillment of a mating preference is a behaviourally mediated mate choice. Other sources of mating bias should not be called ‘mating preferences,’ unless they provide an individual with the opportunity for choice based on a response to the attractiveness of a sensory stimulus. Female rejection of a male that does not provide an appropriate (or attractive enough) display stimulus should not be called resistance, but should be viewed simply as rejection, aversion or disdain. Rejection is a necessary component of mate choice. Female preferences coevolve with male display traits. Resistance, on the other hand, is a behavioural or physiological response to limit the costs of sexual coercion, physical or physiological manipulation or harassment of a female, and it will coevolve in response to male attempts to assert sexual control [43]. Failure to prevent unwanted matings with coercive males is not mating preference, but it could be convenience polyandry—when females accept unwanted mating to minimize the cost of harassment [44]—or simply a reflection that females can be overcome by males’ superior

strength or numbers (see [45], for a discussion of a similar distinction between direct and indirect mate choice).

When preference—the behavioural response to the sensory perception of a secondary sexual display trait—and resistance—an aversive response to physical sexual coercion—are defined in appropriate terms, they can be clearly distinguished as potentially distinct mechanisms contributing to the outcome of sexual selection.

Clear distinctions between preference and resistance, and between display and coercion are particularly important when all these phenomena occur in the same system and within the same individual, as we will discuss in waterfowl. Theoretical models that explicitly incorporate female resistance generated by antagonistic coevolution into existing models of female choice are needed [6], and clearly such models would clarify the dynamics that occur when both preference and resistance occur simultaneously as we discuss here.

(b) Male display and coercion synonymized

Just as narrow sense models of sexual conflict do not properly distinguish female preference and resistance, they also fail to distinguish appropriately between male display traits and male coercion [46]. Narrow sense sexual conflict models have implicitly viewed male display and sexual coercion as a continuum. For example, male forced copulation in garter snakes (*Thamnophis sirtalis*) has been explained as being the result of male exploitation of a female sensory bias response to stress [46]. According to this idea, the males are exploiting the female's need for oxygen when they asphyxiate females during attempted copulation to force them to gape their cloaca [46]. Perversely, a female's need to breathe is redefined as a sexual sensory bias. It is clear that the existence of a physiological need to breathe and the neurological experience of asphyxiation in the context of mate choice are not productively viewed as a pleiotropic effect of natural selection on some other function sensory system. The mass mating behaviour of male *T. sirtalis* is more easily explained as evolving from intrasexual selection and not as a result of intersexual selection via sensory bias.

The narrow sense synonymy of male display and male coercion ignores the fact that display traits and coercion can coexist independently, be deployed in strategic combination and evolve independently within a single species. For example, *Drosophila* have elaborate courtship displays that coexist with and evolve independently from coercive male ejaculate proteins [47,48]. No scientific account of the reproductive behavioural ecology of *Drosophila* could succeed without recognizing these distinct features of phenotype evolving under different forms of selection. To explain the breadth of sexual conflict phenomena, independent definitions of male display and coercion are required. A male display can be defined as a component of the male phenotype (i.e. morphology, behaviour, etc.) that is subject to sensory evaluation by a female in the context of mate choice. Male sexual coercion is any component of the male phenotype that functions in bypassing or subverting female

sensory evaluation and mate choice. Sexual coercion severely restricts female choice, and it typically involves cases where males pursue, catch and restrain females and forcefully copulate with them [49].

Although any female trait that discriminates against one male in favour of another is in conflict with the reproductive interests of the male she rejects [50], it is male behaviour that distinguishes display from coercion, not a female's response to that behaviour. A rejected male can cease display, increase display or abandon display for physical coercion of the female and completely bypass her mating preference.

Kokko [10] developed an intersexual selection model that appropriately recognized the difference between female preference and resistance. However, her model merely redefined the male 'trait' as physical dominance. Although it is an improvement over previous models (see §2c), Kokko [10] does not capture the full, appropriate complexity of male phenotype as potentially including secondary sexual display traits that are independent of social dominance and sexual coercion. Thus, this model does not go far enough to explain the full range of sexual conflict to include the independent forces of both intersexual and intrasexual selection.

(c) Sensory bias and sexual conflict

Sensory biases were a fundamental component of the chase-away model of sexual selection and the original narrow sense sexual conflict models [9,14], and they remain a feature of many narrow sense sexual conflict hypotheses. The existence of sensory biases that can result in sensory exploitation of females by males has become a prominent explanation for the evolution of male traits that have negative fitness effects on females [4,46,51]. However, we argue that sensory exploitation is unlikely to explain many of the observed examples of SAC. Furthermore, failure to distinguish female choice and resistance, and male display and coercion are consequences of the overemphasis of chase-away as the evolutionary source of male traits that are involved in sexual conflict [4,46]. The most influential sexual conflict models have all examined conflict exclusively in terms of female preference in the absence of intrasexual selection through male–male competition (e.g. a pre-existing preference that causes the female to mate at suboptimal levels [9,11,13,20]). In this framework, males merely overstimulate females (exploit their sensory biases), and never coerce or physically force them to mate; females succumb because they are prisoners of their sensory bias thresholds and therefore they cannot escape male exploitation. The alternative model is that a male trait that is damaging to the female can evolve if it confers an advantage through male–male intrasexual competition in the absence of mating preferences. Although this fact had long been recognized [52], the emphasis on sensory bias as a source of damaging male traits has obscured its importance.

Using a 'sensory bias–display' intersexual selection framework as the sole explanation for the origin of traits involved in SAC [46] excludes many biological instances of sexual conflict where the damaging traits evolve directly via male–male competition, and those

in which simultaneous positive mating preferences and resistance to sexual coercion coexist, such as waterfowl.

Many authors have already noted that a sensory mating bias that creates substantial fitness costs to a female is inherently unstable. Females should quickly evolve to reduce the effects of costly sensory exploitation [53,54]. Holland & Rice [14] review several such examples. Gavrillets *et al.* [9] constrained the evolution of the shape of the female preference function and only allowed it to evolve in threshold. A more realistic model by Rowe *et al.* [20] allowed both the shape and threshold of the female mating preference to evolve in response to the costs of mating. Under these conditions, females simply evolved to ignore the male trait and eliminate the costs, which makes coevolutionary exaggeration of trait and preference unlikely [20]. Female sensory biases must be under strong natural selection for other functions *and* have strong pleiotropic effects on mate choice that cannot be eliminated [46]. There are no data to support this claim. Further, a simulation study designed to explore this hypothesis concluded that natural selection on non-mating behaviours will not be likely to constrain the evolution of mating preferences, and that the evolution of mating preferences via sensory bias is most likely to occur when mating preferences are neutral with respect to fitness [55].

A further problem with sensory biases as the evolutionary source of male traits that harm females is the actual source of the sexual conflict [10]. Suppose that sensory biases lead females to mate too frequently, or too indiscriminately, for their own good as suggested under chase-away [46]. As expected, of course, males will fulfil the female preference, regardless of its fitness effect on females. Where is the conflict? Clearly, the conflict under a sensory bias framework is not *between* the sexes. Although males are benefitting from the female's inability to avoid behaving in a self-damaging way, surprisingly these models really imply that it is the female's own fitness that is in conflict with her own mating preferences. Thus, in narrow sense models, sexual conflict would have to be redefined to exist as conflict *within* females and not *between* the sexes.

Males who are preferred because their traits indicate direct or indirect fitness benefits to females are pursuing the same selfish strategies as those males that embody what females prefer without such benefits. Yet, males with honest indicator traits are not usually considered 'manipulative' or 'exploitative' but merely successful. From the male's perspective, both are pursuing the same exact strategy—attempting to provide a female with what she prefers. This is not manipulation. Manipulation and exploitation are better used to describe those male strategies that specifically prevent a female from expressing her autonomous mating preferences by denying a female the opportunity to choose—e.g. male sexual coercion [49].

(d) *Indirect effects via mate identity*

By viewing sexual conflict exclusively in terms of the *direct costs* to females of high mating rate [4,6,7], narrow sense sexual conflict models explicitly exclude the possibility of any coevolutionary response to male coercion that will enable a female to control *which*

male will sire her offspring without reducing the direct cost of coercive matings. For example, antagonistically coevolved female genital novelties in waterfowl appear to function in preventing the phallus from fully everting inside the oviduct and lowering the fertilization success of forced copulations [26,27], but there is no evidence that these coevolved adaptations to sexual coercion reduce or eliminate any of the direct costs of forced copulations themselves [27]. Such coevolutionary responses to male coercion are defined out of existence by narrow sense models of sexual conflict, because they exclude consideration of the indirect costs and benefits.

With the exception of Kokko [10], existing mathematical models of sexual conflict have explored only those costs to females that are independent of male identity (the so-called phenotype independent costs of [4]). Mating preference is defined so as to exclude specifics of mate identity, and there has been no investigation of the potential consequences of direct and indirect costs that depend on male identity and their interactions in the context of sexual conflict [4]. Although the magnitude of direct selection is larger than the magnitude of indirect selection [4,56] and indirect fitness effects are considered to be part of traditional models of sexual selection [4], analysis of both male identity dependent and independent costs and benefits is crucial to further our understanding of sexual conflict, and its absence has contributed to some of the existing confusion in the field.

In §4e, we discuss in detail one of the most salient debates related to the consideration of indirect benefits in sexual conflict theory: that of whether females benefit or not from conflict interactions. Scepticism about the potential for indirect benefits of resistance to sexual coercion is not justification for defining them out of existence, particularly when theoretical models have shown that they are important [10,56].

3. THE BROAD VIEW OF SEXUAL CONFLICT

(a) *The importance of intrasexual selection*

A genuine understanding of sexual conflict requires simultaneous appreciation of the importance of intrasexual and intersexual selection as evolutionary mechanisms that generate sexual conflict, and that there are distinct dynamics between male display traits and female preferences, and between male coercion and female resistance (figure 1). As Darwin [57] recognized, breeding systems determined largely by male dominance (e.g. elephant seals, *Mirounga* sp.) and female preferences for male traits (e.g. birds of paradise, family Paradisaeidae) result in very different evolutionary dynamics and forms of sexual dimorphism. In these extreme cases, one sex has evolved to overwhelmingly control the outcome of reproductive interactions. The interesting role of sexual conflict theory is in understanding what occurs in the most common intermediate cases in which neither sex can completely determine mating outcomes, and there is a dynamic interplay between intrasexual and intersexual selection mechanisms.

Traditionally, intrasexual selection has been viewed as the outcome exclusively of male–male dominance interactions with females as passive subjects. This might accurately describe extreme breeding systems

with complete male dominance. But in intermediate breeding systems in which females have some opportunities to exhibit mating preferences and males cannot control access to females, males may evolve physical sexual coercion of females through intrasexual selection in their quest to outcompete other males during or after mating. Females will then be likely to evolve active resistance to male sexual coercion and SAC may ensue. The important role of male–male competition in the evolution of male traits that can have detrimental fitness effects on females has been obscured by the overemphasis on sensory exploitation as an evolutionary source of damaging male traits.

Many classic examples of sexual conflict arise from simultaneous or sequential episodes of intersexual and intrasexual selection. Thus, male *Drosophila* are both displaying in intersexual courtship interactions, and competing during post-copulatory intrasexual selection with other males. The former process gives rise to elaborate male display behaviour through mating preferences, and the latter to manipulative ejaculate proteins that affect female mating rate through male–male competition. Simultaneously, behavioural preferences of female *Drosophila* evolve in response to male displays, and female physiological resistance evolves in response to attempts at molecular manipulation by preferred mates.

Thus, in a broad sense sexual conflict framework, sexual coercion evolves through the intrasexual competition among males to be more successful at dominating female resistance mechanisms. Variations in male coercion evolve because they are more successful at overcoming female resistance than the attempts at coercion by other males. This is intrasexual selection.

(b) Female preference and resistance and male display and coercion are independent

Sexual conflict occurs when the independent expression of mating preferences is disrupted, or subverted, through sexual coercion, harassment or manipulation by the opposite sex (see [43], for an interesting discussion of these dynamics in the context of sexual dialectics). It can also occur in the absence of any female preference if males evolve traits that harm females as a consequence of intrasexual competition alone. Coercive male strategies may function through physical, behavioural or molecular mechanisms, and they may act in pre-copulatory, copulatory or post-copulatory periods of reproduction. Traits that facilitate sexual coercion of females and result in female harm can evolve because they further male success in intrasexual competition, without being preferred by females during intersexual interactions. In fact, we argue that intra sexual selection may be the main source of male traits that become important during sexual conflict. For example, large body size may be selected for in male–male competition, but then larger males may also become capable of coercing females more successfully [49].

In this broader sexual conflict framework, female preference and resistance are independent phenotypic characters that evolve through different sources of selection. Preference and resistance can coexist in females and be deployed in a context-dependent

manner. Likewise, male display and sexual coercion are not identical, but can be deployed by the same male at different places and times and will be subject to different sources of selection. Male display traits allow males to fulfil female preferences, whereas male coercion may allow males to subvert them. Male coercion and display traits can coexist, and be used independently or in combination. For example, female waterstriders (Gerridae) vigorously resist coercive copulation attempts by males, and males and females have coevolved grasping and anti-grasping devices in one of the better known examples of sexual conflict [4]. However, male waterstriders in some species also court females and fend off competitors by producing ripples [58], while resistance to copulation is not universal [59]. Male courtship and female preference are independent from female resistance to male copulatory attempts.

Alonzo [60] has shown that sexual conflict in the broad sense can arise in breeding systems with multiple male reproductive strategies. Specifically, in the ocellated wrasse (*Symphodus ocellatus*), territorial males provide paternal care and non-territorial, female-like sneaker males gain some paternity. Females prefer territorial males, but their mate choices are subverted by the sneaker males. Females try to avoid males with too many sneakers around their nest. Sexual conflict in ocellated wrasse arises between the female preference and the alternative sneaker male strategy. Similarly, we argue that sexual conflict can arise when males display alternative reproductive strategies of display and physical coercion.

If direct pre-copulatory male–male competition establishes complete reproductive control by a dominant male, there will be no advantage to elevate mating rate and no selection for female resistance. However, if male–male competition is not completely resolved through pre-copulatory male–male interactions, but continues through competition over mating and fertilization, then there will be selection for males to elevate mating rate. This can lead to the evolution of female resistance, as exemplified in many invertebrate mating systems [61]. Female resistance probably occurs to reduce the direct costs of mating inflicted by males. These direct costs result from male traits that are used by males to out compete other males. Under these conditions, sexual conflict arises over direct costs to females from the male's attempts to increase his probability of paternity.

However, if females have clear mating preferences but do not have full control over mating, then male coercion may evolve as a strategy for those males that are not preferred, or for successful males who can further increase their fitness by coercing additional females. Females are then expected to evolve resistance if coercion has negative fitness effects. Resistance does not require a sensory bias to evolve, but may evolve merely through selection on females to reduce the fitness costs of male coercion.

(c) Indirect selection can have important consequences in conflict interactions

We propose a return to the original broad sense view of sexual conflict as conflict of interest between

individuals of different sexes over control of mating and fertilization [1,8]. A fundamental source of sexual conflict in the broad sense is over *who* will determine the paternity of offspring—females through the free exercise of their mating preferences, or males through dominance and physical coercion.

The fitness costs of male coercion can be both direct and indirect [60]. The direct costs to females of male coercion have been thoroughly discussed [4,6,56,62]. However the indirect fitness costs, that the female incurs from male coercion have received less attention [7,10,60]. Females subjected to coerced fertilizations will suffer an indirect ‘opportunity’ cost of not having been fertilized by their preferred male [1,2,5,10,31,32,43]. Indirect benefits arise automatically when male traits are heritable [34], so direct and indirect benefits must be taken into account in both SAC and conventional female choice scenarios [10]. The ubiquity and inevitability of indirect selection is a crucial factor generally overlooked in discussions of the evolution of female resistance [34]. Even if indirect selection is likely to be weaker than direct selection, indirect selection cannot be ignored or defined out of existence, and the strength of direct selection cannot be assumed. Indirect selection may enhance and accelerate evolution of mate choice for direct benefits [34], and similarly, it may enhance and accelerate evolution of female resistance to avoid costs. Indirect costs may also result in cryptic resistance that functions in the control of fertilization without mitigating the direct costs of sexual coercion (see §4). Two mathematical models have shown that indirect effects can have important consequences for sexual conflict. Cameron *et al.* [56] showed that the indirect good genes benefit could overcome direct fitness costs. Similarly, if indirect benefits via good genes or Fisherian mechanisms are large enough, females could evolve preferences for males that physically harm them, resulting in concurrence rather than conflict [10].

As a null expectation, a coercive male may have a random value for an independent display trait. Alternatively, if males pursue coercive behaviour in response to failure in intersexual mate choice, then coercive males will have an expected trait value that is far from the mean female preference. In both of these instances, the indirect costs to a female of fertilization by a non-preferred male would be high because male offspring will inherit genes for display trait values that are random or far from the mean female preference. Consequently, indirect selection for the evolution of resistance to sexual coercion would be high. Conversely, if male success at coercion and preferred male trait values are highly correlated, then there can be no indirect selection for the evolution of resistance. Males that are preferred have to be genetically different from males that are resisted when they try to coerce copulations in order for resistance to evolve by its indirect benefits. We discuss the related idea that resistance can function as a screen for females to choose more attractive males in §4e.

We argue that female resistance to sexual coercion may evolve to reduce either the direct or indirect costs to female fitness. If female mechanisms of

resistance disrupt coercive fertilizations without eliminating the direct costs of coerced copulations, then female aversion is clearly evolving through the indirect benefit of preventing coercive males from siring the female’s offspring. This situation is exemplified in waterfowl.

4. A CASE STUDY: SEXUAL CONFLICT AND GENITAL COEVOLUTION IN WATERFOWL

Here, we apply the broad sense sexual conflict framework to genital coevolution in waterfowl. Unlike most of the invertebrate species that have been studied as cases of sexual conflict (with the exception of *Drosophila*), the breeding systems of waterfowl include both female mate choice based on male secondary sexual displays, and male coercion through violent FEPCs. Female preference and resistance behaviours are clearly differentiated, as are male display behaviour and coercion. Furthermore, both male and female waterfowl have elaborate genitalia that reveal a strong and dynamic pattern of coevolution [26] (figure 2). The social and anatomical complexity of waterfowl provides a rich evolutionary context for exploring the role of sexual conflict in genital coevolution.

We review the biology of waterfowl, and evaluate both female behavioural resistance to FEPCs and genital coevolution. We argue that behavioural and anatomical resistance in female waterfowl have evolved by sexual conflict in the broad sense with a critical role for selection on females to avoid the indirect costs of forced fertilizations (paid when unwanted males succeed at siring offspring), rather than to screen the quality of coercive males to maximize indirect benefits via better quality offspring, as has been recently proposed [63].

(a) *Waterfowl breeding biology*

Mating biases in waterfowl can arise through both female mating preferences for male display traits and female resistance to male coercion. Most waterfowl species have a pair bond with minimal paternal investment beyond mate defence before incubation [64]. Most waterfowl have complex pre-mating social interactions where females assess different males to choose their mate. In many migrating temperate species, mate choice takes place during the winter and may take weeks [28]. The sex ratio in wintering groups is generally male-biased (references in [65]), and females have ample behavioural opportunity for mate choice. Sexual selection through female mate choice has led to the evolution and diversification of elaborate male secondary sexual plumages [62,66], and displays that include elaborate and functionally integrated movements, derived plumage patches and vocalizations, which have been the subject of foundational studies in animal behaviour [64,67,68]. Once the female makes her choice of mate, the pair will migrate together to the breeding grounds.

Waterfowl are among the few groups of birds where FEPCs are common. Paired females may be subjected to violent FEPCs on the breeding grounds. The degree of FEPCs varies greatly among species [29,69,70]. Groups of males, or a single male, will chase and

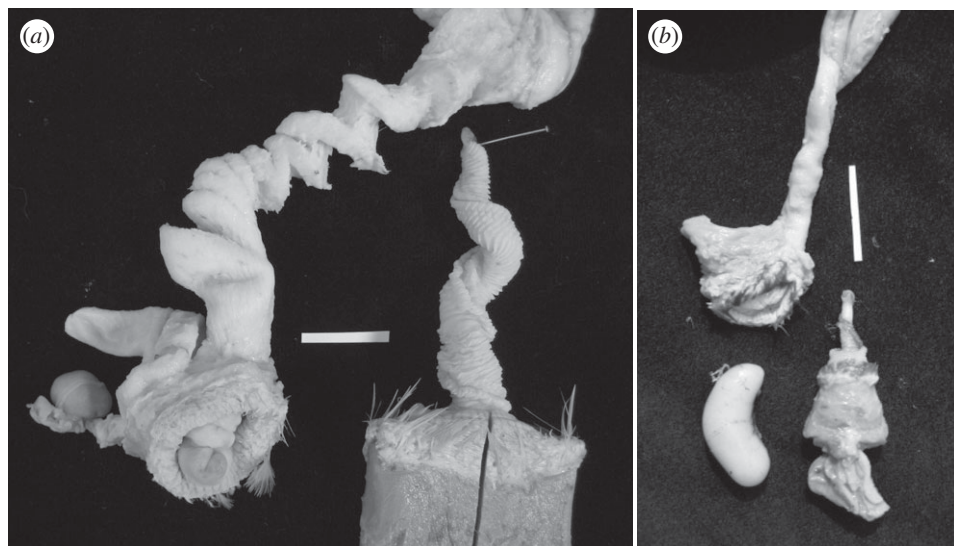


Figure 2. Genital coevolution in waterfowl. In Pekin ducks (*Anas domestica*), in which FEPCs are common, males have a long corkscrew-shaped phallus and females have a convoluted vagina (a), in contrast to the short phallus and simple vagina (b) of harlequin ducks (*Histrionicus histrionicus*), in which FEPCs are absent. More examples of this coevolution are reported in Brennan *et al.* [26]. Scale bar, 2 cm.

subdue a female in or out of the water until they can achieve copulation. Males who attempt forced copulations can be both males that failed at getting a mate for the season, or males who are paired but whose mate is already incubating eggs [29,71]. Female waterfowl strongly resist FEPCs with a variety of behavioural responses, including hiding for hours, undertaking long flights in an attempt to rid themselves of unwanted males and struggling during forced copulations [29,70]. In mallards (*Anas platyrhynchos*), females may choose their mates partly on the basis of their ability to mate guard against FEPCs [72].

Behavioural resistance by females appears to reduce the success rate of FEPCs [73], but in some species up to 40 per cent of all copulations are forced [74]. The direct fitness costs to females from FEPCs are great [73]. Females may lose their social partner and the direct benefits he provides—including feeding territory defence, protection and, in some species, parental care [29,62]. Females may even abandon their current reproductive effort with high levels of FEPCs [75,76]. Finally, females can be injured or killed by males [29]. Female waterfowl have never been reported to solicit extra-pair copulations (EPCs) [70]. Behavioural resistance to forced copulations is nearly universal. The only exceptions are a few instances where forced copulations occurred at the nest while the female was incubating. Under these rare conditions, a female will present her cloaca to a male other than her partner rather than risk breaking all the eggs during a struggle at the nest [29].

The female's mate may actively defend the female by chasing or attacking the coercive males, copulate with her immediately after FEPCs [29,77] or even abandon the female if FEPCs are too frequent [78].

(b) Preference and display versus coercion and resistance

Female waterfowl have clear behavioural preferences for male display traits that are completely distinct

and independent from male coercion [73], and male waterfowl exhibit displays and coercion in a context-dependent manner [70]. Female resistance and preference behaviour are clearly distinct in waterfowl. Female waterfowl demonstrate mate preferences when they have the social opportunity to do so. Consequently, all waterfowl species exhibit distinct courtship behaviours that have evolved through the actions of female mating preference creating a rich phylogenetic radiation [64,67,68]. Furthermore, elaborate repertoires of multiple secondary sexual displays, plumage traits and vocalizations exist in species with both high and low frequencies of FEPCs, and thus with elaborated and reduced levels of male and female genital complexity. For example, wood ducks (*Aix sponsa*), harlequin ducks (*Histrionicus histrionicus*) and buffleheads (*Bucephala albeola*) have elaborate secondary sexual plumage and displays [79–82], but small penises, simple vaginas and few FEPCs [26,69]. By contrast, American ruddy ducks (*Oxyura jamaicensis*), long-tailed ducks (*Clangula hyemalis*) and mallards also have elaborate secondary sexual plumage and displays [80,83,84], but have long penises, complex vaginas (see §4c) and high levels of FEPCs [26,69]. Clearly, female mate preference and female resistance to FEPCs have complex and independent evolutionary histories in waterfowl.

Similarly, male displays and male coercion in waterfowl are completely distinct. Male waterfowl perform ritualized displays to acquire females as mates, and only in some species are FEPCs used as an alternative strategy to increase male reproductive success. FEPCs are performed by males that did not obtain a mate, and by males that were previously paired but whose mate is already incubating [70]. Male waterfowl can use both displays and coercion to increase their fitness.

(c) Genital coevolution

Male waterfowl have variable, elaborate and diverse genitalia [26,69]. Phallus length and elaboration in

waterfowl are positively correlated with FEPCs, so that species with common FEPCs also have long and elaborate phalluses [26,69]. Therefore, phallus morphology probably has evolved through male–male competition [69]. A recent experimental study demonstrated that the penis of male waterfowl shows a phenotypically plastic response to social environment, specifically high levels of male–male competition [85], further supporting the importance of intrasexual competition as a driving force behind genital evolution in this group.

Some female waterfowl have evolved elaborate genitalia consisting of two anatomical novelties—dead end out-pocketings at the entrance to the vagina, followed by clockwise spiralling coils. These vaginal innovations appear to function to selectively limit the extent of intromission of the counter-clockwise spiralling male phallus in the absence of female cooperation (figure 2) [26]. These vaginal structures prevent the full eversion of the penis, but they do not prevent ejaculation because males are able to release sperm from the exposed end at any point along the external sperm channel [27]. A phylogenetically controlled comparative analysis of 16 waterfowl species showed that vaginal elaboration is positively correlated with phallus length, and this coevolutionary process is dynamic [26]. In response to increased phallus length, females evolve increased vagina complexity to retain control over fertilization, which can further select on males to increase phallus length to overcome female resistance and gain paternity. In other lineages, male and female genitalia have coevolved to decrease in size and complexity.

Male–male competition resulting from forced copulations was probably the initial driver of selection on phallus morphology, but subsequent female response in the form of antagonistic genital elaborations has continued to select on phallus morphology, resulting in SAC in waterfowl genitalia.

The alternative, that intersexual selection in the form of male display female preference was the initial driver of selection on phallus morphology, is unlikely. Genitalia regress and regenerate seasonally, and the phallus is still greatly reduced during the winter and early spring months when most species form social pair bonds [86,87]. Seasonal penile regression is accompanied by a drastic reduction in the cloacal musculature and lymphatic machinery that is required for phallus eversion ([87,88], P. Brennan 2008–2012, unpublished data). Although some copulatory-like behaviours are reported to occur during the pair bonding in the winter, these cannot involve female evaluation of the phallus because the phallus cannot be everted at this time (P. Brennan, unpublished data). Further, the penis is kept inside out within the cloaca, and it is only everted during copulation, which occurs in the water.

(d) Sexual conflict in waterfowl, narrow versus broad

Sexual conflict in the narrow sense is an incomplete and inappropriate framework for the analysis of genital coevolution owing to sexual conflict in waterfowl. The narrow sense sexual conflict mechanism hypothesizes that female resistance evolved to reduce the direct costs of coercion, but female behavioural resistance in

waterfowl probably increases the direct costs she pays because males continue to increase their harassment [63,73]. Furthermore, there is no evidence that co-evolved genital mechanisms of resistance reduce the direct costs of coercion. Coevolved vaginal morphologies do not appear to eliminate the post-copulatory direct costs of forced copulations, including exposure to parasites, potential chemical manipulation or damage to the oviduct because the males evert their penis and ejaculate inside the female [27], although these direct costs may be reduced if females can eject ejaculates that are deposited closer to the cloacal entrance. Behavioural resistance to FEPCs has been suggested to be a mechanism by which females maintain the direct benefits of having a partner by reassuring him of his paternity [62,70]. However, males may abandon females when FEPCs are frequent [29,62], behavioural resistance is often unsuccessful, with up to 40 per cent of all observed copulations being FEPCs in some species [89], and the female's mate cannot evaluate cryptic genital mechanisms that the female can use to protect his paternity [63]. Thus, genital coevolution in waterfowl cannot be explained by direct selection alone.

Under our suggested broad sexual conflict framework, complex female genitalia evolve through selection to limit *indirect* costs of coercive copulations by allowing females to reduce the fertilization success of FEPCs. Existing evidence suggests that the anatomical novelties in female waterfowl genitalia appear to function to reduce the likelihood of fertilization by forced copulations [26]. Because these coevolved female genital anatomies appear to function to effect *which* male will sire the offspring, this class of co-evolved female strategies cannot evolve as a result of direct selection alone. If indirect costs of coercion are unimportant, as suggested by the narrow sense view of sexual conflict, then we would not expect females to evolve to control which male sires their offspring. In species of waterfowl with frequent FEPCs, however, females seem to exercise post-copulatory choice against coercive males. Existing genetic evidence shows that the fertilization success of FEPCs is significantly lower than the frequency at which FEPCs occur in all four waterfowl species for which paternity data exist. In the Ross's goose (*Chen rossii*) and lesser snow goose (*Chen caerulescens*), respectively, FEPCs accounted for 33 and 38 per cent of all successful copulations but they result in only 2–5% of young, even though most FEPCs occurred during the laying period [90]. In wild mallards, where up to 40 per cent of observed copulations can be forced copulations [74], only 3 per cent of offspring were produced by 'extra-pair' copulations [91], and even under captive conditions where females are less able to escape FEPCs, only 6–11% of offspring were sired by forced copulation males [91]. In wild Gadwalls (*Anas strepera*), forced copulations are relatively common [92], but only 4 per cent of offspring were produced by EPCs [93]. It is unlikely that within-pair copulations are significantly underreported in these studies, because within-pair copulation in waterfowl is associated with conspicuous pre- and post-copulatory display behaviour [64,67,68]. In addition, several studies have found support for the hypothesis

that males who perform FEPCs are trying to increase their chances of paternity by directing FEPCs to females in the laying and pre-laying phase (captive studies: [91,94], field studies: [78]), and by timing FEPCs to the morning hours as soon as females leave their nest when sperm has a higher chance to outcompete sperm that has been previously stored in her oviduct [95]. These studies indicate that FEPCs are much less successful than within-pair copulations, despite their high frequency of occurrence and behavioural strategies used by forced copulation males that seek to increase their success. A big difference between waterfowl and other birds is that the latter lack a penis and therefore forcible fertilization is not possible. Contrary to the waterfowl, voluntary EPCs in other birds are probably uncommon (or very difficult to detect [96,97]), and extra-pair fertilizations (EPFs) are reported with a frequency higher than expected, given the rarity with which EPCs are observed in socially monogamous species (11–18% EPF rate [98]). That is, in most birds few voluntary EPCs are likely to be very successful in producing EPFs, whereas in the ducks many forced copulations are required to produce a small amount of EPFs.

Low fertilization success of FEPCs may result if the female's mate is able to successfully outcompete FEPCs males via post-copulatory competition. The female's mate often copulates immediately with her after FEPCs have taken place. These copulations usually lack any pre-copulatory displays and are thus known as forced within-pair copulations (FPCs) [71]. However, if paired waterfowl males could reassert their paternity fully, there would be no need for females to evolve complex vaginas. The fact that they do suggests that they play an important role in determining the outcome of fertilization (see [99], for discussion of this type of female control).

Female behavioural and genital resistance in waterfowl are best explained as having evolved through sexual conflict in the broad sense, as females try to minimize indirect costs of male coercion, and reassert their own control over fertilization. The evolution of complex genitalia in waterfowl is probably the result of antagonistic coevolution through sexual conflict in the broad sense. The elaborate male phallus has probably evolved in response to intrasexual competition to succeed at coercive fertilization. Because females cannot behaviourally prevent all FEPCs, complex vaginal structures in female waterfowl have evolved to lower fertilization success of FEPCs by restricting the full eversion of the male penis inside the vagina [26], and therefore lowering the indirect fitness costs that the females suffer from offspring sired by non-preferred males. These indirect costs have been demonstrated in captive mallard ducks, where offspring viability and female fecundity are both reduced when females are not allowed to reproduce with the males they prefer [100], offering further support to the importance of choice in increasing indirect benefits to females.

(e) Resistance as a screen is not viable in waterfowl

A large body of literature has centred on whether female resistance evolves as a result of sexual conflict

or as a form of female choice for superior mates (also known as 'resistance as a screen', or 'resistance as choice') [50,101–103]. According to this hypothesis, open-ended female resistance will ensure that a female copulates only with dominant males that are best able to overcome female resistance; male offspring will be superior competitors/coercers, and female resistance will evolve through the indirect benefits of their superior coercive male offspring [50,101–103]. This type of screening has been hypothesized to occur during pre-copulatory struggles, and during and/or after copulation via cryptic female choice mechanisms [50]. The main argument against the resistance as a screen hypothesis is that the magnitude of the direct costs imposed by coercive males may be much greater than the magnitude of any potential indirect benefit that females may gain [56], but this issue is far from being resolved. For example, if indirect benefits are strong enough, females can evolve preferences for males that physically harm them, resulting in concurrence (or benefits of resistance) rather than conflict [10].

But what are the selective advantages of female resistance? So far this question has been answered either in terms of the indirect fitness *benefits* of being coerced into mating (i.e. resistance as a screen), or in terms of the reduced direct costs of unwanted copulation as proposed by narrow sense sexual conflict [50,56,101–103]. The problem is that that these are not mutually exclusive hypotheses. Even if resistance allows females to avoid the direct costs of coercion, females still could produce sons that are better at forcing copulations if resistance fails only with the most coercive males, or if females eventually cease resisting the most coercive males. The question however is whether the potential indirect benefit could be significant enough to *drive* the evolution of female resistance, and this has remained a contentious issue [56], despite the possibility that resistance can indeed function to prevent the males less capable of forcing females from achieving copulations.

We argue that female resistance evolves through broad sense sexual conflict to limit the *direct and indirect fitness costs* of coercion, whereas in resistance as a screen, resistance evolves to maximize the *indirect fitness benefits* of coercion. In contrast to the earlier-mentioned, these two hypotheses are mutually exclusive and therefore testable [35]. Female resistance may not be perfect. Despite a female's best efforts at resistance, males may overpower them and may successfully sire offspring. Offspring of successful coercive males may be better at coercion than other males in the population. The question, however, is whether the female would have done better if she had been able to freely choose the sire of her offspring [104], and there is mounting evidence that this is indeed the case.

In mallards, it has been shown that the viability of offspring produced as a result of female choice is higher than offspring produced when females were bred with an unpreferred male [100]. More recent studies have begun to address whether the negative fitness effects of coercion and harassment can include cross-generational effects, where the offspring

produced by females as a result of coercive encounters can have even lower fitness measures [105,106], further suggesting that coercive encounters can negatively affect both direct and indirect fitness.

Adler [63] suggested that female resistance in waterfowl has evolved to screen male quality and that females receive indirect benefits by biasing paternity to more manipulative males (those who can succeed at coercion). The natural history of waterfowl and the data on waterfowl mating systems indicate that it is unlikely that female resistance has evolved as a form of choice in waterfowl.

First, if there is direct competition among males to succeed at sexual coercion, then the direct costs of resistance will increase proportionally with the indirect benefits of resistance because males who are more successful at forcing copulations will inevitably impose higher direct costs on the females they coerce. As it has been shown for the original formulation of Zahavi's handicap principle, there are substantial barriers to evolution when the benefits are directly proportional to the costs [107,108].

Furthermore, any potential indirect benefit of siring male offspring that are better at forcing copulations will be reduced by half because half of the offspring will be females, who will then be subjected to the same direct costs of coercion [109]. In waterfowl with high rates of FEPCs for which there are genetic data, the proportion of offspring sired as a result of FEPCs is very small (2–5%; data reviewed earlier) [74,91,92], so indirect benefits are likely to be extremely small, especially in comparison with other sons that have inherited sexually attractive traits of the preferred mate, which probably compose half of the remaining 95–98% of all offspring. The vanishingly small percentage of male offspring produced by coercive matings (1–2.5%) is unlikely to compensate for the substantial direct costs of being harassed by males who are better at forcing copulations themselves.

A previous reviewer suggested that genetic data documenting the low success rate of FEPCs was good evidence of strong selection for the indirect benefits to females of sexual coercion as only a few coercive males are expected to be good enough to bypass female resistance. In order for this to be the case, female preferences and resistance would have to be optimized simultaneously to maximize the indirect benefits of intrapair and forced extrapair fertilization. Coercing males experience a success rate of only 2–5% in comparison with other copulations. This differential success constitutes strong intrasexual selection on male coercion, which is exactly the source of selection in our proposed mechanism for SAC by broad sense sexual conflict. However, for female resistance to actually evolve by the indirect benefit of coercion, it would have to proceed through the 2–5% success rate of FEPCs over all copulations. Given the relative weaknesses of indirect benefits, it is very unlikely that the indirect benefits of resistance from a few percent of young will be more important than the indirect benefits of reasserting female choice, which derive from 95–98% of offspring.

Finally, female waterfowl exhibit independent mate choices and forced copulation resistance behaviour

and anatomy. In a species with mate choice, resistance as a screen will only evolve if the males that successfully coerce females are different from those males that females prefer. Under captive conditions, however, female mallards do not change their receptivity to FEPCs according to any of the coercing male's traits [73], so female resistance is unlikely to have evolved for females to screen male quality. This issue raises a new problem because male secondary sexual display traits are often hypothesized to be indicators of quality or condition, and high quality and condition are often assumed to be positively associated with physical dominance and success at coercion. Coercing male ducks may either have unpreferred trait values or random trait values, because protection against fertilization by forced copulation can only evolve if successful coercing males are different from the males that females prefer. So, if the displays communicate any information at all, they cannot communicate the same dimensions of quality or competitive ability that are advantages in sexual coercion.

5. IS THE APPLICATION OF A BROAD FRAMEWORK USEFUL OR PRACTICAL?

The narrow view of sexual conflict was originally intended to set sexual conflict into the broader context of sexual selection [6], and it served to diffuse the criticism that sexual conflict was nothing new because we had always known that the evolutionary interests of the sexes differ [103]. Under both sexual selection and conflict, male traits spread because they confer a fitness advantage to the bearer. However, the distinction between sexual conflict and sexual selection is that sexual conflict results from sexually antagonistic selection between interacting male and female phenotypes [5].

The emphasis on the avoidance of direct costs of mate choice in the narrow sense sexual conflict and chase-away model was consistent with some of the best known examples of conflict, including *Drosophila* and bed-bugs (family Cimicidae), where mating *per se* is costly for females and the costs increase rapidly with multiple mating because of male inflicted harm [4]. In species where female choice has never been documented (for example, bed bugs [110]), it is possible that mitigating mating harm is the only important component of female fitness once she has obtained enough sperm to fertilize her eggs (but it is important to recognize that this still does not provide evidence of the chase-away mechanism). However in those species in which male displays, female choice, male coercion and female resistance are all present and distinct, observable biological phenomena—such as *Drosophila*, waterfowl, many mammals (including humans) and perhaps even some waterstriders—both direct and indirect selection are likely to be important in determining female fitness. Understanding the evolution of these organisms will require explicitly adopting the broad sense of sexual conflict, which includes consideration of both direct *and* indirect fitness benefits to females, and defines preferences as distinct from resistance and display traits as distinct from coercion. Accordingly, SAC can occur when females evolve

traits to minimize either the direct or indirect fitness costs of male sexual coercion.

The difficult part of implementing this broad framework is that it will require an in-depth understanding of indirect selection, something that we have yet to achieve even in the more developed models of sexual selection. However, as waterfowl suggest, the evolution of genital mechanisms of female resistance through indirect benefits of the control of paternity provide a new source of data on likelihood of indirect selection itself. Studies of sexual selection and sexual conflict will overlap in order to understand the behavioural and morphological complexities that we see in nature, because sexual conflict is about the special evolutionary interactions that occur when the processes of intrasexual and intersexual selection clash.

6. CONCLUSION

In species where females exercise affirmative mate choice, female resistance may evolve by broad sense sexual conflict to reduce the direct and indirect costs of coercion. When females are physically unable to prevent male sexual coercion, there will be selection for copulatory and post-copulatory anatomical and physiological mechanisms of female discrimination that allow females to remain in control of paternity to reassert their choice. These evolutionary responses can set the stage for an evolutionary arms race between the sexes.

Distinguishing between female resistance as choice and female resistance as conflict is not possible with a narrow framework of sexual conflict that considers only the direct costs of unwanted copulations to females, but it is possible with a broad view of sexual conflict. We propose: (i) that consideration of the identity of the male is central to conflict; (ii) that most traits that are involved in sexually antagonistic races originate as the result of male–male competition and not of a sensory bias; and (iii) that female resistance is evolutionary independent from female preference. This broad framework to study sexual conflict allows us to explain traits that were previously excluded from conflict such as the evolution of female post-copulatory traits that function only to lower male fertilization success rather than to minimize direct costs to females. Consideration of how male identity influences the outcome of sexual conflict via direct and indirect benefits is central to understanding conflict, and most studies of conflict interactions would benefit from this addition. We also argue that failure to distinguish resistance and choice has prevented a full understanding of the evolutionary processes that influence female behaviour, especially in species where females express both.

We hypothesize that the evolution of complex genitalia in waterfowl is the result of SAC through sexual conflict in the broad sense. The elaborate male phallus has probably evolved in response to intrasexual competition to succeed at coercive copulations. Because females cannot behaviourally prevent all FEPCs, complex vaginal structures in female waterfowl have evolved to lower fertilization success of FEPCs by impeding the eversion of the phallus during copulation and lowering the indirect fitness costs that

the female will suffer if her offspring are sired by non-preferred males.

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