Behavioural ecology of sexual autonomy and the case of protection against risky courtship

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Abstract

Evolutionary changes and interspecific diversity in sexual coercion and autonomy are often linked to indirect selection on mate preferences. Yet, this approach overlooks the small fraction of indirect selection in total selection on mate choice and assumes unnecessarily specific conditions in the recent 'autonomy-enhancing' risk-reduction model. This paper proposes a more parsimonious approach based on direct selection and basic signalling theory, incorporating ecological variables to better explain sexual biodiversity. Particularly, the spatial dimensionality of mating environments is emphasized for its role in enhancing sexual freedom through both diminishing monopolization and elevating escape potential from sexual coercion. Empirical evidence, ranging from waterfowl to humans, seems to better align with this ecologically constrained signalling perspective. Furthermore, it suggests that choosers keep coercion risk at ecological baseline by leveraging their escape potential. This repositions intriguing protective elements like bowerbirds' constructions as courtship features that have been bargained to respect sexual autonomy rather than enhancing it through indirect selection. It implies that courtship induced risks, such as reduced mobility, may in principle increase substantially precisely because they are offset by protective measures. Future research could reveal the prevalence of such risk-balancing strategies, advancing our understanding of mating dynamics. This work suggests new theoretical and empirical research avenues within the ecology of mating dynamics.

Keywords

sexual coercion, sexual autonomy, mate choice, courtship, escape potential, mating strategies

Introduction

Considerable interspecific differences exist in sexual coercion, monopolization, and mate choice. For example, bowerbirds exhibit virtually no sexual coercion or monopolization; females freely choose their mates based on complex courtship displays that include elaborately decorated bowers as well as vocal and visual performances (Borgia, 1995). In contrast, other taxa experience heightened sexual coercion and reduced mate choice, occasionally escalating into sexual arms races. A notable example is found in some waterfowl species, where males have evolved intricate penile morphologies to facilitate forced fertilization. This is counteracted by females through the evolution of complex genital tracts that obstruct unwanted fertilization (Brennan et al., 2010).

Recently, the interspecific diversity in coercion and sexual autonomy has been attributed to an indirect benefits mechanism of mate choice (Snow et al., 2019; Snow & Prum, 2023). Specifically, Snow and Prum (2023) posit that, given sufficient random heritable variation in both female mate preferences and male display traits, certain species incidentally evolve a new female preference for a male trait that concurrently diminishes the male's coercive capacity. According to that hypothesis, once embarked upon this evolutionary trajectory, females 'remodel'—or reduce—male coercive capacity to enhance their sexual autonomy, thereby sidestepping sexually antagonistic coevolutionary arms-races. Snow and Prum (2023) contend that this remodelling, despite being costly for males, persists because females choosing such coercion-reducing traits are likely to reap indirect benefits through having attractive mates. Crucially, Snow and Prum's (2023) indirect benefits model, resonating with Fisher's runaway and sexy sons hypotheses, presumes an 'intrinsic' driver: it assumes female mate preferences exert indirect selection on themselves and coevolve with attractive male traits independently of any extrinsic factors or selection sources (Prum, 2010).

This article challenges the view that incidental forking paths lead either to arms races or to an intrinsic coercion-reducing process, presenting instead a more parsimonious and biologically realistic perspective. To this end, the concepts of female escape potential and male monopolization potential are first introduced, emphasizing that interspecific variations in male coercion and female behavioural freedom can be convincingly attributed to discernible ecological disparities, rather than to random coincidence. Furthermore, theoretical and empirical research on the evolution of mate choice suggests that indirect selection is less parsimonious, more controversial, and weaker than direct selection on mate preferences, particularly concerning sexual coercion which incurs high direct costs. Thus, this article advocates for a direct selection framework based on basic signalling theory, taking into account ecological influences. This approach offers a more plausible explanation for the contrasts between waterfowl and bowerbirds than the one proposed by Snow and Prum (2023). Specifically, the behavioural freedom afforded to most avian species, including bowerbirds—chiefly through their capability of flight—enhances female escape potential while simultaneously reducing male coercive abilities, a dynamic less pronounced in waterfowl due to their aquatic adaptations. Furthermore, this framework introduces an alternative model, the 'ecological bargaining' model, which posits that choosers use their inherent ecological escape potential as a bargaining chip to demand protective measures that mitigate increased risks during courtship, such as temporarily reduced mobility. This suggests that the protective courtship elements highlighted by Snow and Prum (2023) should be viewed as autonomy-respecting, rather than 'autonomy-enhancing' traits.

Although Snow and Prum (2023) extend their intrinsic model to hominins, this article argues that disparities in mate choice, male coercion, and monopolization in this taxon – which obviously also includes contemporary humans – are more aptly elucidated by this alternative perspective as well. In this context, it should be cautioned that sexual agency, coercion, and monopolization are sensitive topics. An approach that considers the impact that naturally occurring ecological factors may have on the roles these sexual facets play in human societies may be deemed controversial. However, both shying away or endorsing a theory based on its palatability, risks conflating objective understanding, grounded in rational theory, with subjective understanding, rooted in relatability and moral justification. As Moore (1922, p.45) cautioned, conflating objective and subjective understanding can lead to the 'appeal to nature' fallacy, a pitfall that must be avoided. Yet, a clear distinction between them is often difficult to make. Therefore, attempts at, for instance, objective understanding of the ecology of sexual coercion should not be mistaken for endorsement of that behaviour.

Disentangling male monopolization and female escape potentials

The potential for male monopolization of females or the resources necessary to attract them, tends to increase the frequency and intensity of male-male contest competition. Moreover, when males successfully restrict access to potential mates for their rivals, the cost effectiveness and opportunities for mate choice, sexual coercion, and sperm competition are significantly curtailed (Pradhan & van Schaik, 2009; Puts, 2010). Several factors underpinning male monopolization—whether achieved solitarily or via coalitions—such as the spatial and temporal clustering of females and resources have been considered (Emlen & Oring, 1977). However, the spatial dimensionality of habitats may be an especially impactful ecological factor (Janik & Slater, 1997; Pradhan & van Schaik, 2009; Puts, 2010). Defence against competitors might be feasible in primarily one-dimensional environments (like burrows) or two-dimensional landscapes (such as dry land); however, the challenge intensifies in three-dimensional habitats, like trees or air, where myriad entry points exist. In two-dimensional spaces, the complexity of repelling rivals increases linearly with the defence area's radius. Conversely, in three-dimensional spaces, it escalates with the square of the radius (Puts, 2010).

Discernible aspects of habitat and biology, particularly the spatial dimensionality of mating environments, do not only influence male monopolization potential but also female ability to evade harassment. Empirical evidence across various taxa—including primates, reptiles, and birds—supports the intuitive notion that the effectiveness of male coercive strategies wanes too as the environment's dimensionality affords females increased mobility (Pradhan & van Schaik, 2009).

Disentangling male monopolization potential and female escape potential unveils an important distinction between, respectively, weapons and coercive organs, a nuance overlooked by Snow and Prum (2023) who conflate them under the umbrella term ‘weapons’. Commonly, weapons (or 'weaponry', which encompasses sexually dimorphic size, strength, and aggression) are defined as sexually dimorphic traits primarily selected for their ability to enhance success in intrasexual contests or combats, including morphologies such as tusks, horns, and antlers (Pradhan & van Schaik, 2009; Rico-Guevara & Hurme, 2019). Conversely, ‘coercive organs’ can be characterized as sexually dimorphic features designed to subdue or force females into mating, which neither improve success in male–male combat nor elevate the possessor’s allure to the opposite sex. Examples include grasping organs like the antennal claspers found in water striders and intromittent organs such as penises, common among mammals and reptiles. While weaponry may have a secondary role in coercion, coercive organs (by definition) do not confer advantages in contests with other males (Pradhan & van Schaik, 2009). Therefore, the evolution of weaponry is primarily influenced by male monopolization potential, whereas the evolution of coercive organs depends on female escape potential.

In environments where both monopolizing weapons and coercive organs lose their effectiveness—particularly evident in three-dimensional habitats—ornamentation often emerges as a strategy to attract mates (Pradhan & van Schaik, 2009). Ornaments, commonly defined as sexually dimorphic traits appealing to the opposite sex, encompass a variety of mostly conspicuous features, including vivid colorations, distinctive morphological features, and acoustic, visual, or tactile performances (Andersson, 1994; Darwin, 1871).

Mind manipulation

Recent investigations of male coercion and female mate choice have typically built on indirect selection models (Pradhan & van Schaik, 2009; Snow et al., 2019; Snow & Prum, 2023). Pradhan and van Schaik (2009) assume that ornaments evolve because preferring them confers choosers indirect benefits in terms of viability of offspring (i.e., good genes), while Snow and Prum (2023) assume a ‘mere’ attractiveness mechanism of coercion reduction (i.e., sexy sons or Fisherian runaway). However, it has been shown that the distinction between good genes and Fisherian models is spurious and the tendency to treat them as mutually exclusive, misguided. Instead, indirect selection is a general process in which fitness components trade-off along a continuum (Eshel, 2000; Kokko, Brooks, Jennions, et al., 2003; Kokko et al., 2002)

Furthermore, there are compelling reasons, particularly in this case, to prioritize a direct-selection-based explanation over one based on indirect selection. Direct selection models are more parsimonious, and direct benefits typically overwhelm indirect benefits. Natural selection can influence any trait, either directly or indirectly. Direct selection occurs when the traits themselves, including mate preferences, enhance fitness. Conversely, indirect selection on mate preferences involves additional conditions: it depends on the strength of direct selection on the courter's traits, the magnitude and direction of the genetic correlation between the preferences and traits, and the ability to inherit the directly selected traits (Kokko, Brooks, Jennions, et al., 2003). Thus, the strength of indirect selection is reduced by the genetic correlation between the preference and the fitness benefits conferred by the chosen mate. Theoretical work supports that indirect selection tends to be weak and is often overshadowed by direct selection on mating preferences (Kirkpatrick, 1996; Kirkpatrick & Barton, 1997; Kotiaho & Puurtinen, 2007). Empirical studies confirm these theoretical predictions (Rosenthal, 2017). For instance, a meta-analysis by Møller and Alatalo (1999) found that less than 2% of variation in offspring viability was attributable to variation in preferred traits. Similarly, Arnqvist and Kirkpatrick (2005) found no evidence of indirect selection on female preferences in the context of extra-pair copulations, and another meta-analysis by Møller and Jennions (2001) demonstrated that the effects of direct benefits generally exceeded those of good genes.

Moreover, if indirect selection is generally weak and overshadowed by direct selection, this should be particularly evident in cases of sexual coercion, where the direct costs—including severe outcomes like physical trauma and death—are high. Therefore, the interspecific diversity in sexual coercion and the resulting variation in mate choice autonomy are unlikely to be happenstance outcomes of indirect selection. Instead, they are more plausibly the predictable consequences of ecological factors.

From a basic signalling theory perspective, ornaments essentially evolve to manipulate the mind of potential mates toward mating, and as a more cost-effective alternative to physical manipulation like coercion. Crucially, this manipulation is to the signaller's and possibly but not necessarily the reactor's advantage (Dawkins & Krebs, 1978). Snow and Prum (2023) argued that certain taxa avoid sexual arms races, stumbling upon an alternative evolutionary path. However, basic signalling theory instead suggests that those taxa just shifted the nature of these contests to a mental, rather than physical, arena. Moreover, these evolutionary shifts thus seem empirically and theoretically more likely to be induced by changes in habitat and naturally selected biology (Pradhan & van Schaik, 2009; Puts, 2010), rather than a consequence of intrinsic sexual selection dynamics (Prum, 2017; Snow et al., 2019; Snow & Prum, 2023). That is, in certain ecological settings, such as three-dimensional environments enabled by flight, mind manipulation through ornaments becomes relative more cost-effective than physical manipulation through weaponry or coercive organs.

Unlike previous approaches to sexual coercion, which imply quite particular pathways (i.e., a specific kind of indirect benefits in the case of Snow and Prum, 2023), the present framework doesn't lock into a single hypothesis in advance, allowing for multiple, non-exclusive causal mechanisms of mate choice.

The basic signalling perspective does not exclude the possibility of indirect benefits from the outset. For instance, theoretically, a female mate preference could confer genes that enhance offspring fitness—representing indirect benefits and a way for the female to benefit from mind manipulation too (i.e., 'honest signalling'). However, unlike previous models, this framework does not prioritize these indirect benefits, considering they typically represent only a small fraction of the total selection pressure on mate preferences and corresponding traits (Rosenthal, 2017). Instead, it focuses on how ecological settings influence sexual negotiations and the more parsimonious and biologically realistic assumption of the significant direct fitness costs of sexual coercion.

Male monopolization and female escape potentials are positively related to male-male contest competition and female mate choice, respectively, while they both tend to be negatively related to sexual coercion. Therefore, when considered concurrently, they elucidate the disparate taxonomic distributions of male coercion, female mate choice, male-male contest competition, and their associated phenotypic traits (Pradhan & van Schaik, 2009). For instance, this perspective illuminates the puzzling discrepancy between birds and mammals regarding ornamentation and weaponry (Darwin, 1871), positing that the prevalence of ornamentation in birds arises because avian females, capable of flight and tree habitation, can more adeptly evade male harassment. Conversely, terrestrial male mammals are often more extensively equipped with weaponry, a trait likely attributed to the females' limited escape capabilities, and particularly, a heightened male monopolization potential (Pradhan & van Schaik, 2009). It should be evident, however, that we are talking about patterns and not laws, and there can be many exceptions to this pattern. Yet, many of these exceptions are potentially explainable when other ecological aspects are factored in, such as predation risk, food distribution and population density. Hence, phylogenetic comparative analyses should be employed to empirically investigate how the complex interplay of such ecological factors constrains sexual selection dynamics.

An ecological bargaining model

Snow and Prum (2023) apply their model to bowerbird courtship, using it as a prime example. Male bowerbirds create specialized courtship structures – known as bowers – to curtail their own opportunities for forced copulations, as originally suggested by Borgia (1995). For example, the 'avenue bower', characterized by its parallel stick walls, fosters a safeguarded space wherein females can evaluate the male's elaborate courtship decorations and performances from a position of security. Snow and Prum (2023) construed these bowers as evolving through their proposed coercion-reducing, indirect selection mechanism, labelling them as female 'autonomy enhancing traits'. Furthermore, they cite additional examples of purported autonomy-enhancing traits: The rearward-oriented elements of several displays, such as males of various manakin genera approaching females in a backward orientation; in birds of paradise, the elaborate courtship displays performed upside-down by male *Paradisaea rudolphi* as well as the positioning of *Seleucidis melanoleuca* and *Ptiloris victoriae* on broken trunks to be approached by females from below.

While these are intriguing examples of potentially protective elements, they do not specifically support the indirect benefits model proposed by Snow and Prum (2023). Instead, given the inherent abilities for flight and arboreal living, akin to most avian species, these birds inherently navigate within spherical environments—granting virtually unrestricted movement in all directions and, subsequently, an elevated escape potential relative to terrestrial species. Aligned with this notion, forced copulation is notably scarce among volant birds, bowerbirds included (Adler, 2010; Borgia, 1995; McKinney & Evarts, 1998). This scarcity invites an alternative explanation for the evolutionary trajectory of protective male display elements like bowers. Rather than mitigating male coercion through weak indirect selection, it is posited here that they are directly selected by females to simply safeguard their already substantial escape potential. In essence, the ability to fly provides these female birds with a strong bargaining position to demand protection and avoid the costs of risky courtship. Focusing on the bowerbird case, ecological, behavioural, and phylogenetic data support the ecological bargaining model over Snow and Prum's autonomy enhancement model.

First, their model predicts that net coercion risk is comparatively lower in species with more protective display elements because it interprets these elements as lowering the base line coercion risk thanks to incidentally stumbling on a coercion-reducing, protection producing evolutionary pathway. In contrast, the ecological retention hypothesis anticipates no such negative relationship. Rather, it predicts that protective elements function to counterbalance any courtship induced coercion risks to maintain a consistent net coercion risk/escape potential across contexts. While Borgia's (1995) study on bowerbirds inspired the indirect benefits enhancement hypothesis (Prum, 2017; Snow & Prum, 2023), it rather supports direct benefits ecological bargaining. It suggests a positive, counterbalancing association between male aggression and protection. Specifically, the protective bowers of spotted bowerbirds are conjoined with "aggressive elements [in male displays] not observed in other species" (Borgia, 1995, p. 1). Furthermore, when experimentally removing the protective wall, males reduced the rate of aggressive behaviours, indicating that males adjusted the intensity of their display in relation to the protection available to the female. Borgia (1995, p. 11) himself concluded with emphasizing "proximate benefit explanations", in terms of protection from forced copulation, for the evolution of bower building.

Second, a phylogenetic comparison between bowerbird species as discussed by Prum (2017) hints at a conceivable generalized scenario of gradual coevolution between incrementally intricate decoration arrangements, inviting meticulous female inspection, and protective bower structures. Snow and Prum (2023) autonomy enhancement model implies that this gradual evolution towards more protection not only gradually lowers net coercion risk but was incidentally initiated as well. In contrast, the principle of retention of pre-existing female escape potential implies that compensating protection has permitted male courtship to transition from the ancestrally spherical mating environment, provided by flight and arboreality, to a hemispherical mating environment. The latter encompasses decorated courts that invite proximate inspection only if it does not infringe upon the pre-existing female behavioural freedom to exercise mate choice. Recent phylogenetic investigations indicate that bower building evolved twice, in parallel, in bowerbirds (Ericson et al., 2020). If coercion reduction is initiated incidentally, as the enhancement hypothesis entails, there is no special reason to expect it to have occurred twice within phylogenetically proximate species. Conversely, under the premise of retaining base line escape potential, the parallel coevolution of protective elements and extravagant decorations in closely related lineages sharing low predation risk and plentiful food resources is a plausible, ecologically granted outcome (Diamond, 1991).

Snow and Prum (2023) interpret the captivating protective display elements in bowerbirds and other birds as autonomy enhancing traits, resulting from indirect selection. However, these elements are predominantly found in the courtship displays of flying, arboreal birds—species endowed with a high pre-existing escape potential. This article contends that a more parsimonious and empirically supported explanation is that these protective elements are directly selected by females to mitigate the high costs of coercion and to preserve their inherent escape potential. Therefore, 'autonomy-respecting traits' might be a more apt term to describe these fascinating protective elements in the courtship displays of manakins, birds of paradise, bowerbirds, and potentially numerous other taxa.

Ecologically granted behavioural freedom (such as arboreality and flight in birds) enable females to avoid the direct fitness costs of sexual coercion. This can drive simultaneous or 'co-selection' of courtship elements that would otherwise increase coercion risk (e.g., attractive elements inviting close inspection), and protective elements that inhibit coercion, ensuring that their net impact doesn’t increase coercion risk. An intriguing extension of this principle might be seen in the expansive train of the peacock, potentially acting as a ‘mobile bower’. Traditionally, this spectacular plumage has often been interpreted as a handicap (a mating trait that reduces survival chances) preferred by females purportedly because handicaps are indicators of heritable viability (Zahavi's 'handicap principle', 1975). However rather than - or in addition to – showing off self-limitations to escape from predators or parasites, it might serve to self-limit coercion during close inspection, thereby aligning with females’ behavioural tendencies to evade unwanted mating. This perspective does not only bring forth the notion of 'autonomy respecting traits' as an enrichment to the understanding of the evolution of courtship displays but also introduces a multifaceted lens that perceives extravagant traits as not merely costly signals of quality or attractiveness but also as self-limiting traits respecting and aligning with pre-existing female behavioural autonomy.

For clarity, we can finally formalize the autonomy retention principle as follows:

$$A_{net} = A + (B - C)$$

In this straight-forward equation:

- *A* is *Inherent Coercion Risk*: This component represents the baseline coercion risk level, inherent to the ecology and biology of the population. For example, in many volant and arboreal bird species coercion risk is minimal, thanks to an elevated escape potential in an essentially spherical mating environment (see Fig. 1a)

- B is *Additional Coercion Risk*: This component represents the contingent risk introduced by escape potential reductions that result from the particularities of the male's strategic courtship morphologies, behaviours, contexts and so on. For example, some (extended) ornaments may invite close inspection, such as the meticulously arranged male bowerbird courtship decorations, which requires females to forsake the ecologically afforded safety of their spherical habitat and approach the courter on the ground, basically a hemispherical mating environment (see Fig. 1b).

- C is *Protection against Additional Coercion Risk*: This component represents the female's counterstrategies. These are courtship elements that females directly select to counterbalance the increased risk introduced by certain male courtship traits.

- A_{net} is *Net Coercion Risk*: This component represents the net risk after accounting for the inherent and additional coercion risks and the protective measures. It's the actual risk faced by the female in the context of these interacting strategies.

The fundamental assumption of the proposed ecological bargaining principle is that any increase in B is counterbalanced by an increase in C, ensuring that $A_{net} = A$. Within the sexual conflict paradigm, this model illustrates an evolutionary arms race. Females leverage their inherent escape potential (reflected in A as an ecological constant) to mitigate male-imposed coercion risks (B). The protective elements (C) are not merely passive defences but actively bargained tools in the sexual conflict. This perspective highlights the active role of females in negotiating sexual interactions. Thus, viewing these dynamics through a game-theoretical lens, the model represents a strategic bargaining game between males and females. Females utilize their escape potential as bargaining power, demanding the addition of counterbalancing protective elements to male displays in response to increased potential risks. This scenario resembles a Nash Equilibrium in evolutionary games, stabilized by ecological baseline coercion risk (A) as a result of which neither sex can unilaterally improve their reproductive success without considering the other's strategy. The model thus encapsulates a sophisticated negotiation process, with both sexes adapting their strategies to maintain reproductive fitness. Despite the possibility of huge courter-induced elevations of contingent coercion risk (B), when inherent chooser's escape potential or baseline risk (A) is high, it will enforce evolutionary stability by leveraging equally huge counterbalancing protective countermeasures (C) (see Fig. 1).

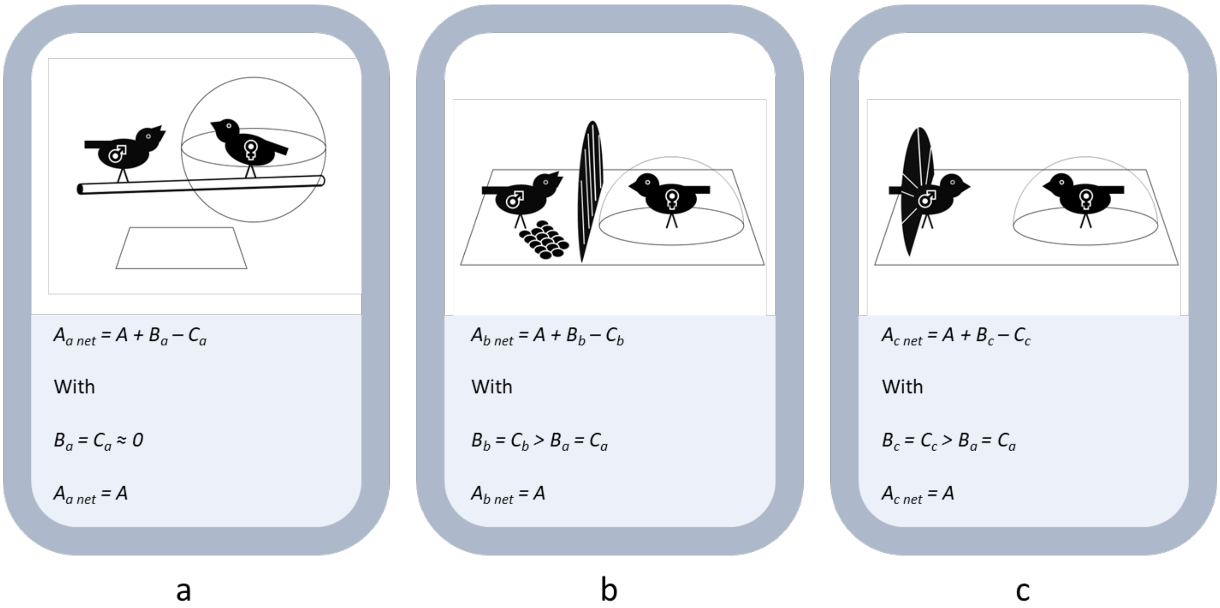

Fig. 1 *The ecological bargaining principle posits that females will not relinquish their ecologically ensured sexual autonomy (baseline coercion risk A). Consequently, any increase in coercion risk (B) in courtship scenarios is accepted by females only if offset by protective courtship features (C), preserving their intrinsic escape potential. This ensures that Net Coercion Risk (A_{net}) remains at the ecologically established baseline (A) across various mating contexts (a, b, and c). Panel a illustrates species with minimal coercion risk due to a three-dimensional mating environment, such as many volant and arboreal species, enabling high escape potential. Panel b demonstrates how females may momentarily compromise their spatial advantage, as seen in bowerbirds, yet maintain safety through selectively demanding protective structures like bowers, using their pre-existing escape potential as a bargaining tool. Panel c suggests that the peacock's elaborate train serves as a 'mobile bower,' handicapping male mobility and thereby reducing coercion risk during ornamental inspection in a hemispherical mating space*

Hence, evolutionarily, females leverage their ecological escape potential across various contexts to neutralize the significant direct fitness costs of increased coercion risk with protective measures. On a proximate level, contingent on the required behavioural flexibility and cognitive sophistication, females are likely to reject any male advances that include elements increasing risk unless these are instantaneously offset by protective elements during a courtship sequence (MacGillavry et al., 2023). This hypothesis could be tested through experimental manipulation of risk-increasing and protective elements in courtship behaviours. Indeed, experimental evidence suggests that such proximate risk-balancing negotiations occur in bowerbirds (Borgia, 1995).

Furthermore, while Snow and Prum's remodelling (2023) implies a progressive evolutionary reduction of net coercion risk once it kicks in, ecological bargaining predicts that if ecological conditions remain constant, net coercion risk remains constant too. The predictions of evolutionary stability versus reduction of coercion could for instance be verified by using phylogenetic methods comparing basal with more derived taxa in a phylogeny. In addition, another prediction particular to this alternative perspective is that the higher the baseline escape potential, the more room there is for relative reductions in this potential, which in turn provides the opportunity for the evolution of more extreme protective measures to compensate for those reductions. Consequently, protective traits are expected to be more frequent and more extreme in taxa where choosers' behavioural freedom is inherently high and mate choice tends to be elevated, such as in volant birds, jumping and flying insects, aquatically mating mammals, and fish, where courters compete for mates in three-dimensional environments (Amorim et al., 2015; Janik & Slater, 1997; Pradhan & van Schaik, 2009; Puts, 2010).

Finally, it should be noted that the broader framework of physical and mental manipulation in sexual bargaining does not preclude some level of deception, possibly creating slight differences between baseline and net coercion. For instance, great bowerbirds create a forced perspective illusion from the female's viewpoint. Males maintain the positioning and orientation of objects to create a positive object size-distance gradient, which has been sometimes misinterpreted as making the male appear larger than he is (Doerr & Endler, 2014; Endler et al., 2010, 2014; Kelley & Endler, 2012a, 2012b, 2017). This interpretation illustrates the persistent bias towards 'good genes' explanations that overlook evolutionary trade-offs between weaponry and ornamentation, adhering to assumptions that 'bigger is better because fitter and therefore more attractive.' However, a negative gradient effect on objects at the distant end of the decorated court makes them appear farther and thus larger. Conversely, maintaining the positive gradient could make the displaying male appear smaller than he actually is to visiting females, which he might do in response to the female's avoidance of coercion.

Compared to spotted bowerbirds from the same genus, great bowerbirds experience higher rates of bower destruction and decoration theft due to the closer proximity of their mating arenas (Borgia, 1995). While size may be selected as weaponry to fend off rivals, and thus confer advantages in tightly packed leks, it can secondarily be used to coerce females more effectively (Pradhan & van Schaik, 2009). This creates a trade-off similar to that observed in men's sexually selected traits, where dominance signalling (effectiveness in contests) increases linearly with a lower voice pitch. However, attractiveness reaches its peak at 96 hertz and declines as the pitch drops further (Saxton et al., 2016). Evidence suggests that some species' females prefer smaller males (Pradhan & van Schaik, 2009). Thus, it might be that the males of this largest bowerbird species may have 'resolved' this dilemma of opposing selection pressures by creating a forced perspective theatre that makes them appear smaller and less threatening to visiting females, while still maintaining the size necessary to defend their arenas successfully. Previously, it was found that the 'quality' of the positive gradient—actively and strongly maintained at varying levels by individual males—is associated with mating success (Kelley & Endler, 2012a, 2012b). Rather than reflecting genetic quality, these patterns might indicate that the larger the male, the higher his mating success due to successful rivalry, and the steeper the positive gradient required to obscure his more intimidating size from females. This hypothesis could be tested by measuring the sizes of displaying males and relating them to mating success, contests, and forced perspective gradients.

Waterfowl – an avian exception

Snow and Prum (2023) endeavoured to elucidate the divergent evolutionary paths between waterfowl, characterized by intense genital arms-races, and avian taxa, such as bowerbirds, birds of paradise, and manakins, where mating systems are predominantly guided by female mate choice. The implication that a protective function may not be limited to bowerbird structures and that it might occur more commonly and widely than previously acknowledged is intriguing. However, this article argues that their confinement to an intrinsic, self-reinforcing indirect benefits mechanism from the outset is unnecessary or even unwarranted, and quite likely flawed. By explicitly excluding external sources of selection on mate choice (Prum, 2010), their intrinsic mechanism necessitated their ascription of divergences in the latter taxa from waterfowl to mere coincidence, stating: "We hypothesize that a new female mating preference for a novel male trait *incidentally* correlated with lower effectiveness of sexual coercion can evolve because it disrupts [the initial] equilibrium [between female mate choice based on male display and male sexual coercion in determining fertilization] in favour of female mate choice, reducing the efficacy of sexual coercion, and expanding female sexual autonomy" (p. 2, my emphasis).

However, as noted, these variations are broadly concordant with expectations derived from pre-existing ecological and biological disparities among bird taxa. A pivotal moment in avian evolution, the advent of flight, facilitated a departure from the two-dimensional constraints of dry land, ushering species into three-dimensional mating environments. This transition notably amplified female escape potential and concomitantly curtailed male coercive capacities, manifesting in a conspicuous scarcity—or even absence—of forced fertilization across a majority of bird species (Adler, 2010; McKinney & Evarts, 1998). Furthermore, this adaptation into aerial environments likely inhibited male monopolization potential. Although approximately 90% of bird species exhibit social monogamy (Lack, 1968), a discernible disparity with sexual monogamy is apparent. Extrapair copulations are notably prevalent and documented across avian species, with extrapair offspring identified in 90% of species explored (Griffith et al., 2002). This pattern of unsuccessful monopolization of mates, in synergy with elevated female escape potential, catalysed the dominance of female mate choice, not only among polygynous taxa like bowerbirds, but also permeating intra- and extrapair mating behaviours among socially monogamous species.

Yet, in certain instances, the avian mating environment's dimensionality diminished, potentially constraining female behavioural freedom and/or amplifying male monopolization, with consequent ramifications on mating systems. Waterfowl may present an exemplification of this dynamic, their mating environments reduced in dimensionality due to being non-arboreal and tethered to localized critical resources like ponds, essentially confining them to hemispherical, nearly two-dimensional, habitats (McKinney & Evarts, 1998; Pradhan & van Schaik, 2009). The complex biomechanical trade-offs between adaptations to aerial and aquatic locomotion further restrict the behavioural freedom of waterfowl that navigate both mediums (Elliott et al., 2013). Moreover, while waterfowl have evolved specific adaptations for water take-off, the intrinsic physics—encompassing buoyancy, surface tension, and lack of traction—can be expected to stringently inhibit female escape potential, thereby potentially further enhancing male coercive opportunities. Impact of such intrinsic physics on behavioural freedom and sexual autonomy could be experimentally and empirically further investigated.

Additional ecological factors, notably population density and food clustering, might channel the consequences of the reduced dimensionality of their habitats roughly into two main waterfowl groups: territorial species, like the Tundra Swan, and non-territorial duck species like the Mallards (Prum, 2017). While waterfowl exhibit social monogamy reminiscent of most birds, especially non-territorial species show a distinctive pattern with respect to extra-pair copulations, with male coercion coming into play – a phenomenon documented in 55 species across 17 genera, which equates to approximately one-third of all waterfowl species (Adler, 2010; McKinney & Evarts, 1998). This stands in marked contrast to the prevailing autonomous (extrapair) mate selection found in other bird species and is not simply a happenstance occurrence, as implied by Snow and Prum (2023). Instead, due to significantly lowered female escape potential, coercion is a feasible alternative male reproductive strategy, occasionally escalating into sexually antagonistic genital arms-races (Brennan et al., 2010). Moreover, due to increased male monopolization potential, and consistent with contest competition overriding all other sexual selection processes (Puts, 2010), in many of the waterfowl species where forced extrapair copulation seems to be absent, males manage to defend exclusive breeding territories (McKinney & Evarts, 1998). Phylogenetically controlled comparative analyses, considering aspects like population density, food clustering, and spatial dimensionality of the mating environment may reveal whether hypothesized interactional effects between these ecological factors on mating strategies hold.

The hominin case

Snow and Prum (2023) also extrapolate their remodelling mechanism to primates, particularly concerning the reduction of dimorphism and aggression and the increase in prosociality among hominins. However, it should be noted that, contrary to being substantially ‘deweaponized’ as per Snow and Prum’s depiction, hominins display sexual traits broadly aligning with anticipated terrestrial primate patterns related to female escape and male monopolization potentials.

Manifestations of sexual coercion, male-male contests, and ornamental reduction notably amplify among terrestrial primates, correlating with diminished female escape potential and enhanced male monopolization, in comparison to arboreal species, as indicated by evidence on forced copulation (Smuts & Smuts, 1993), sexual dimorphism in body and canine size (Leutenegger & Cheverud, 1982; Plavcan & van Schaik, 1997), Pan conflict behaviour (De Waal, 2007; Goodall, 1986; Puts et al., 2023), sexual dichromatism (Crockett, 1987), duetting (Geissmann, 2000; Verpooten, 2021), and mate preferences (Cooper & Hosey, 2003; Cowlishaw, 1996).

Consistent with hominins increasingly committing to terrestrial life since at least the Pleistocene (Finlayson, 2014), contests predominantly account for the evolution of most human male secondary sexual traits. To mention but a few examples, men, compared to women, exhibit, on average, greater stature, strength, and craniofacial robusticity, along with a higher tendency towards risk-taking, outgroup discrimination, and involvement in dyadic and coalitional violence. A wealth of these and other sexually dimorph traits, which typically mature or intensify at sexual maturity, are aligned with having been shaped by contest competition for mates, as they predict success in male contests, mating, and reproduction (Puts et al., 2023).

While Snow and Prum (2023) underscore the minimized size dimorphism in humans as a sign of reduced weaponry, it is pertinent to delve deeper into the composition of such size differences. Although minimal sex differences in mass (under 20%) might suggest subdued male contest competition throughout human evolution (Fuentes, 2021), the uniquely large fat stores in human females—uncommon among primates—deserve consideration, especially as they likely don't contribute to physical contests as effectively as muscle and lean mass do (Puts et al., 2023). Notably, human males showcase approximately 33% more lean mass and possess 61% and 75% more total and upper-body muscle mass than females (Abe et al., 2003; Lassek & Gaulin, 2009). Such disparities seem to align more with human skeletal dimorphism, which even surpasses that of chimpanzees (*Pan troglodytes*) – a species known for their aggressive male dominance contests within groups (Plavcan, 2012).

In addition, while there is a recognized diminution in canine size and canine dimorphism in humans (Prum, 2017; Snow & Prum, 2023), it's pertinent to consider the evidence indicating a conceivable evolutionary transition in the male phenotype. The data suggests a movement away from the ancestral reliance on large canine teeth and biting towards a more profoundly weaponized 'extended phenotype', guided by the coevolution of lethal handheld weapons, hand proportions, and bipedalism (Darwin, 1871; Dawkins, 1982; Puts et al., 2023; Young, 2009).

Further, despite the exceptional level of human prosociality within primate contexts, there persists a compelling historical thread of male–male violence in the human lineage, substantiated by phylogenetic, paleontological, and archaeological data and aligning with terrestrial primate contest competition. Across human societies, lethal male violence and mating competition are correlated, men significantly surpass women in both perpetrating and falling victim to lethal violence (95% of same-sex homicides), resonating with patterns observed among other great apes (Puts et al., 2023). Moreover, in alignment with diminished environmental dimensionality, sexual coercion emerges as a tangible strategy among human males, thereby placing constraints on female mate choice (Puts et al., 2023; Wilson & Daly, 2009).

However, the striking behavioural variation among human's closest relatives should not be overlooked. Bonobos (*Pan paniscus*), equidistantly related to humans as chimpanzees, provide a counterpoint to the typical image of male aggression in great apes. These 'make love not war' apes as primatologist Frans de Waal fittingly called them (Weinstein, 2016), stand out not just from primates but social mammals in general, due to their low levels of male dominance and aggression, exceptional sexual freedom, and the formation of intimate bonds among unrelated females. Thus, while chimpanzee and bonobo behaviours are broadly consistent with an arboreal/terrestrial habitat, significant differences in monopolization, coercion, and sexual autonomy call for further scrutiny. Research increasingly indicates that ecological factors, similar to those observed in waterfowl, such as food availability and population densities, are key drivers behind these behavioural divergences.

Compared to chimpanzees, bonobos experience more stable food availability (partly due to less seasonality). While this ecological aspect probably cannot account for all sexual behavioural differences between the two Pan species, it does seem to have a significant impact. Crucially, food stability likely reduces both within- and between-group feeding competition, with various downstream effects on sexual phenotypes (Walker & Boehm, 2020; Wrangham, 1993). Within bonobo groups, food stability supports a pattern of high gregariousness among females, in contrast to the more variable social patterns observed in females of chimpanzee communities. Such gregariousness has facilitated the evolution of striking intrasexual affiliative socio-sexual behaviours, unique to female bonobos (Lee et al., 2021).

Between-group competition is also mitigated among bonobos, and this may also have been facilitated by an ecological history of more stable food availability (Wrangham, 1993). While male chimpanzees form strong social bonds to coalitionary defend territories where females reside and food is available, male bonobos do not strongly bond (Emlen & Oring, 1977; Surbeck et al., 2017). Consistent with this, male lethal violence, a cost-effective means to monopolize mates by eliminating rivals when population densities are high, occurs more commonly between than within groups in chimpanzees, while it is virtually absent in bonobos (Wilson et al., 2014). Furthermore, as only humans and chimpanzees were originally known to engage in lethal raiding, this specific form of intercommunity violence was hypothesized to be an ancestrally inherited predisposition. However, it was subsequently shown that also distantly related spider monkeys engage in this violent intergroup strategy, whereas equidistantly related bonobos don't, suggesting that the cause of the difference is rather to be found in socio-ecological conditions than shared ancestry (Aureli et al., 2006). For one thing, unlike bonobos, spider monkeys exhibit strong male bonds as well, which are marked even by homosexual behaviours, similar to the socio-sexual behaviours among female bonobos (Busia et al., 2018).Moreover, the occurrence of bonobo intercommunity food sharing suggests mitigated feeding competition on the between group level, indeed (Fruth et al., 2018).

Thus, the ecological factor of stable food availability likely contributed to the bonobo pattern of strong female bonding and weak male bonding. In combination with the Pan pattern of male philopatry, this might have created the opportunity for the especially strong mother-son bond to emerge, characteristic of bonobos (Surbeck et al., 2017). All this may have facilitated female bonobo's sexual autonomy. While male chimpanzees curtail female mate choice through coercive mate guarding and aggressive intimidation (Muller et al., 2011), bonobos exhibit virtually no sexual coercion (Paoli, 2009). Initially hypothesized to result from the strong female alliances (Wrangham, 1993), it appears that the lack of sexual coercion among female bonobos may rather stem from co-dominance and affiliation among males and females (Paoli, 2009; Surbeck et al., 2017). At the same time, continual access to females (in mixed-sex feeding parties) and the weak connection between ovulation and swelling may have reduced the effectiveness of sexual coercion as a male reproductive strategy (Hohmann & Fruth, 2003; Walker & Boehm, 2020). Hence, this brief comparative review contrasting bonobo behavioural sexuality with that of other primates, highlights that socio-ecological factors may account for substantial variation in coercion, mate choice and monopolization, even among closely related species.

An increasingly terrestrial habitat may have contributed to the fact that levels of human contest competition and sexual coercion remained similar to chimpanzees and much more elevated than those of bonobos, despite the potential mitigating effects of increasingly efficient resource extraction in the human lineage. Yet, it seems clear that monopolization and coercion have not negated the influential role of mate choice throughout human evolution either. Evidently, mate choice has sculpted the (extended) phenotypes of both human sexes, aligning with theories of mutual mate choice and cooperative parental care (Puts, 2010; Stewart-Williams & Thomas, 2013). Unlike other great apes, humans seem to have a history of cooperative breeding, social monogamy, and related behaviours, which makes us rather appear 'featherless birds' than 'naked apes' in those respects (Martinho-Truswell, 2022). This potentially accounts for instance for the lack of clear sex differences in musical and artistic prowess, attributes that may have partially evolved as extended ornaments (Marin, 2022). It is therefore of interest to investigate whether any elements, analogously to the protective bowers of bowerbirds, are incorporated in human ornaments and courtship dynamics to counterbalance any elevated coercion risk beyond ecological baseline. On a different note, we should cautious not to overestimate the historical prevalence and importance of human ornaments relative to armaments. Given the substantial augmentation of human extended phenotypes, attributed to massive cultural transmission and economic expansion, it is crucial to compare relative investments in ornaments versus armaments with other species, thereby providing context to humans' remarkable ornamental achievements, like monumental religious architecture and entertainment industries, both of which have been facilitated by increasingly elevated resource extraction.

Finally, as underscored, the presented extrinsic behavioural ecology framework does not negate the potential influence of other ecological factors, aside from dimensionality, on the breadth of women's behavioural freedom either (Pradhan & van Schaik, 2009). Various factors may indeed alleviate male coercion and monopolization throughout human evolution as well. Evidence indicates similar ecological influences as discussed in waterfowl and the Pan genus, such as resource availability and population density, on female behavioural freedom, including the exertion of mate choice. Regional variations in population density in pre-modern periods, influencing available land, are correlated with regional variations in patrilocality (male philopatry) versus matrilocality (female philopatry), with the latter granting greater female behavioural freedom. Patrilocal clans, protecting valuable herds and lands and bequeathing them to sons, often idealized female seclusion. In contrast, where land was abundant, women experienced greater mobility and could attain status as esteemed authorities (Evans, 2023; Hudson et al., 2021). Similarly, economic development across Eurasia elevated the cultural significance of romantic love, veering away from the tradition of arranged marriages and thereby liberating female mate choice from familial constraints (Baumard et al., 2022).

Thus, even in post-agricultural periods, (sexual) behaviour, norms and autonomy have been continuously moulded by a tapestry of ecological pressures. These factors are not peripheral even to the social and legal advances that promote women's autonomy; rather, they are intricately entwined. Sexual agency, then, must be seen as a confluence where ecological affordances, economic structures, and cultural norms coalesce. In acknowledging this, we gain a comprehensive view of the societal progress observed in human history, emphasizing that ecology, in its broadest sense, continues to be a vital player in shaping human behaviour and social structures.

Conclusions

Expanding on evidence that bower wall building may have evolved to protect females against sexual coercion (Borgia, 1995), recent research has drawn attention to a potentially wider prevalence of protective elements in courtship across species (MacGillavry et al., 2023; Snow & Prum, 2023) . However, this article invites reconsideration of the attributed 'mechanisms'. Rather than resulting from 'remodelling', an incidentally initiated, intrinsic form of indirect benefits (Snow & Prum, 2023), interspecific disparities may be more aptly interpreted through a fundamental signalling perspective that incorporates extrinsic ecological factors, primarily the spatial dimensionality of the mating environment. The latter notably influences both male monopolization and female escape potential, thereby shaping sexual selection across species (Pradhan & van Schaik, 2009; Puts, 2010). This basic viewpoint prioritizes direct selection over indirect selection on mate preferences and corresponding traits. Theoretical and empirical research supports that direct selection typically overpowers indirect selection, which tends to be weak at best (Arnqvist & Kirkpatrick, 2005; Kirkpatrick, 1996; Kirkpatrick & Barton, 1997; Kokko, Brooks, Jennions, et al., 2003; Kotiaho & Puurtinen, 2007; A. Møller & Jennions, 2001; A. P. Møller & Alatalo, 1999; Rosenthal, 2017). This is particularly relevant to the high direct fitness costs of coercion.

Furthermore, while remodelling unrealistically assumes that indirectly selected protection reduces coercion below a species' initial baseline, an 'ecological bargaining' model suggests that the direct female fitness costs of coercion stabilize sexual negotiations at the ecological baseline. Essentially, choosers may appear to compromise their autonomy, yet maintain baseline safety through demanding for the inclusion of protective courtship elements, leveraging their inherent escape potential as a bargaining tool. This perspective not only resonates more closely with previously considered cases, waterfowl, bowerbirds, and humans (Snow & Prum, 2023)—but is also theoretically more parsimonious and less controversial by eschewing commitment to a spurious indirect benefits model of female mate choice from the outset (Kokko, Brooks, Michael, et al., 2003; Kokko et al., 2002). Table 1 summarizes the main differences between the models.

Table 1. Summary of Main Differences Between the Remodelling and Ecological Bargaining Models

Model	**Remodelling (Snow & Prum, 2023)**	**Ecological Bargaining**
Mate choice model	More controversial, less parsimonious, and weak indirect benefits of mere attractiveness	Least controversial, more parsimonious, and stronger direct benefits (i.e., basic signalling theory)
Cause of interspecific variability	Intrinsic coincidence	Predictable extrinsic ecological conditions
Predictions about protective elements	Indirectly selected to reduce baseline coercion	Directly selected to maintain net coercion risk at ecological baseline
Empirical evidence	Little support for (this specific kind of) indirect selection of protection	Preliminary but promising support for the notion that protection is bargained to offset risky courtship

Despite the fundamental insights garnered from avian studies, a potential risk lurks in neglecting the unique attributes of the avian taxon. In a broad spectrum of the animal kingdom, mate choice does not occupy the same paramount status as it does in birds. To illustrate, while a significant corpus of sexual selection research centres on mate choice, contest competition presents approximately equivalent prevalence—or rarity, given that merely 12% of animal phyla exhibit either ornaments or weapons (Wiens & Tuschhoff, 2020). Even within the sphere of human behavioural evolution, the weight afforded to indirect benefits female mate choice—particularly when juxtaposed against contests—may be overestimated (Puts, 2010; Puts et al., 2023; Saxton et al., 2016). Consequently, future work, including mathematical modelling and phylogenetic meta-analysis, should ideally adopt a wide taxonomic viewpoint, foster models that incapsulate more fundamental models of mate choice than excessively specific indirect benefits, include other mating strategies as well such as sexual coercion and monopolization, and take into account the potentially interactive effects of various ecological factors such as spatial dimensionality, resource availability, predation risk and population density. Although it might be challenging to gather the necessary data, phylogenetic comparative analyses may reveal that substantial interspecific variation in mating strategies can be attributed to the interplay between predictable ecological pressures and constraints.

In conclusion, this article advocates renewed focus on how ecology shapes and constrain mating strategies across species. Specifically, this work argues that choosers utilize their ecological escape potential from sexual coercion as strategic leverage to neutralize risks associated with courtship scenarios. In this light, protective courtship features are reinterpreted as traits that respect the chooser's inherent sexual autonomy. Continued research in this field could unveil the widespread prevalence of such elements, enriching our understanding of the ecology of mating dynamics across species.[1]

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[1] AI-assisted technology has been used for language editing purposes in this research.

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