The inconvenient truth about convenience polyandry

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Abstract

In the last two decades molecular techniques have revealed that polyandry, or multiple mating by females with different males, is common. One explanation is that females engage in convenience polyandry, mating multiply to reduce the costs of sexual harassment. Although the underlying logic of convenience polyandry is clear, and harassment often seems to influence mating outcomes, it has not been subjected to as thorough theoretical or empirical attention as other explanations for polyandry. Here, we re-examine convenience polyandry in the light of a new generation of studies showing previously unconsidered benefits of polyandry. We suggest that true convenience polyandry is likely to be a fleeting phenomenon, but a phenomenon that can profoundly shape mating system evolution due to potential feedback loops between resistance to males and the costs and benefits of mating.

The history of polyandry

Mating systems are often classified as either monogamous, with a single male paired with a single female, or polygamous, with multiple mates of one or the other sex. Polygamy in turn can be subdivided into polygyny (one male with multiple females) or polyandry (one female with multiple males; see glossary). The near ubiquitous nature of polygyny has never been debated, but polyandry has had a somewhat contradictory history. On the one hand, researchers using insects and other invertebrates as study organisms have often acknowledged the prevalence of multiple mating by females [1]. In vertebrates, however, polyandry has been seen to require pair bond formation between one female and multiple males, with commonly cited examples including some wading birds, pipefish and dendrobatid frogs. Such long-term associations are rare in vertebrates, and hence polyandry was viewed as an anomaly, with the rationale being that a female could be fully inseminated by a single male, making multiple mating with different males unnecessary. These taxon-wide generalities led to inherent contradictions running through the two streams of literature, with polyandry either being viewed more as the norm (in insects [2]) or a rare evolutionary exception (in birds and mammals [3]).

In the last two decades, however, advances in molecular techniques for assaying paternity have resulted in a more integrated perception of female mating behaviour. Multiple mating and extra-pair copulations by females are all-but ubiquitous, even in species once thought to be strictly monogamous [4]. Polyandry is no longer regarded as a rare phenomenon, involving, for example, sex role reversal and paternal care in the vertebrates, but as a common mating system where females engage in copulations with multiple partners [4-5]. This conceptual shift has led to the 'polyandry revolution' [5] - a surge in studies seeking to untangle the myriad evolutionary causes and consequences of female multiple mating. As a result, the reasons that females engage in polyandry have been widely discussed [5], bringing a welcome expansion of mating system theory.

Importantly, the idea that females engage in polyandry not to gain benefits, but rather to limit the costs imposed upon them by harassing males, has been discussed throughout the polyandry revolution. This hypothesis is known as convenience polyandry [2], and while it continues to be highlighted by those seeking to understand why females engage in multiple matings [for recent papers see: 6-17], we argue that it would benefit from more rigorous theoretical and empirical testing that other, benefits-driven hypotheses for the evolution of polyandry, have been subject [16-22].

The polyandry revolution has demonstrated that females are by no means passive players in sexually antagonistic co-evolution [23-24] and if they are able to escape harassment in less costly ways than by mating, then they will [25-27]. What is more, if indirect genetic benefits invariably follow from polyandry [17], such convenience polyandry, where the only benefit is cost mitigation, might be rare and fleeting. In this review, we consider recent theoretical and empirical developments in polyandry research in order to critically reappraise the convenience polyandry hypothesis.

What is convenience polyandry?

The benefits of coercive strategies to males are relatively clear, but female strategies for curtailing the costs of harassment are more ambiguous [6]. Convenience polyandry is a commonly cited example of such a strategy. The traditional definition of convenience polyandry is that females accept superfluous matings to reduce the costs of harassment, such that they 'make the best of a bad job' [2; 6]. We define convenience polyandry as follows:

Convenience polyandry occurs when females increase their receptivity to mating based on the relative costs of resistance and mating, such that they are more likely to mate when the costs of resistance or avoidance exceed the net costs of mating.

The convenience polyandry hypothesis is intuitive - attempting to resist superfluous matings with persistent males can be more energetically demanding, can reduce time available for other necessary activities (foraging, ovipositing, etc.) and can even result in more physical damage (including death), than accepting the mating (see Figure 1). Although some good examples of convenience polyandry exist in nature (see Box 1), the hypothesis has not been elaborated upon theoretically (even though the coevolutionary consequences of sexual harassment and resistance have been extensively modelled, these dynamics are not equivalent to the convenience polyandry hypothesis). Moreover, when convenience polyandry is typically described, it is usually treated as separate from direct or indirect benefits explanations for female multiple mating.

Likewise, convenience polyandry is only occasionally empirically tested, and tends to be inferred from observations of high female mating rates at high male densities [10; 15; 31]. This interpretation is based on the idea that more frequent encounters with males result in elevated resistance costs for females, but the relative costs of resistance compared to mating are seldom separated or measured explicitly (and see [32] for an outstanding example). The logic of convenience polyandry is compelling, but we still need to measure resistance costs and map them to different behavioural or ecological contexts in order to understand why the female mating rate is subject to evolutionary change. We suggest that convenience polyandry should only be ascribed when the costs of resistance have been shown to exceed the net costs of mating, such that there is strong evidence for cost mitigation. Below we describe new findings in support of our contention, and their implications for convenience polyandry, which we use to suggest a framework in which to test it (see Table 1).

What if polyandry is the null hypothesis?

Despite, or perhaps because of, the ubiquity of polyandry, active female multiple mating, as opposed to passive acceptance of matings in the face of sexual harassment, is sometimes regarded as an anomaly that requires an explanation [7]. It has been suggested that societal biases regarding appropriate or expected female behaviour might have a role to play in such interpretations (42-43; see Box 2). However, this idea is also based on the founding principles of sexual selection theory. Bateman's principles, based on work in *Drosophila melanogaster*, state that females gain less reproductive success per mating than males [44], and so high levels of polyandry are not expected. Although the robustness and applicability of Bateman's conclusions have been called into question [see 43; 45-46], the general acceptance of this paradigm (which may itself have a socio-cultural component; 42; see also 47) has meant that the evolutionary significance of polyandry was, until relatively recently, overlooked.

The polyandry revolution, however, has shown that monandry is rare compared to polyandry, and recent work has demonstrated, both theoretically and empirically, that there are many, less clear-cut reasons for females to engage in polyandry [7; 9; 19-22; 33; 49-57]. Moreover, the idea that polyandry is unexpected, and the implicit treatment of monandry (and by extension convenience polyandry), as the null hypothesis has been increasingly called into question, perhaps most explicitly by Kokko & Mappes ([33] see Figure 2). Using a modelling approach, they found that even when mating carried fecundity or longevity costs, polyandry was predicted to predominate over monandry. A key assumption in their models was that female receptivity was consistent for each encounter with a male, such that the probability of acceptance did not change over a female's lifetime. Thus the risk of dying a virgin, combined with a lack of information about future encounters, made polyandry the most likely strategy, even if the optimal life history strategy under perfect knowledge and free access to mates was monandry.

What is more, other bet-hedging strategies that promote genetic diversity [17] and genetic compatibility [49], or ensure fertility under inbreeding [49] or outbreeding [9], might mean that polyandry is the optimal strategy for an individual to adopt because it spreads the risk of mating failure [19; 33; 51-52]. Moreover, polyandry can be advantageous to populations, for instance reducing extinction risk by purging mutation load, increasing effective population size [53] and rescuing populations from the effects of inbreeding [22]. Indeed, the importance of polyandry in preventing extinction has been demonstrated in populations of *Drosophila pseudobscura* harbouring a selfish X-linked drive [54].

These alternative functions for polyandry mean that it might be selectively favoured even if it does not maximise the fitness of individual females under all circumstances, because it can minimize the risk of mating failure. Under bet-hedging, a monandrous female might have very high fitness (if mating is costly) but the risk of mating failure (either because she fails to mate entirely or does not mate with a compatible male) means that she could have zero fitness [19; 33; 51-52; 55]. A polyandrous female, on the other hand, might never experience such high fitness (if mating is costly), but the risk of complete reproductive failure is lower. In this way, polyandry might persist in the absence of individual benefits, and even when it is costly to females (see [19; 51-52; 58-59] for more on bet-hedging and polyandry).

If polyandry arises because of a baseline level of receptivity that ensures fertility, but leads to multiple mating across the population, then we should re-evaluate the convenience polyandry hypothesis. First, the absence of benefits can no longer be taken as suggestive of convenience polyandry, because polyandry is just the null expectation. Second, convenience polyandry can no longer be inferred from increased female mating rates when the sex ratio is more male-biased, as Kokko & Mappes [33] demonstrate. To counter the risk of mating failure, if females are equally receptive to every mating attempt, then this means that they will mate with a set proportion of all males they encounter. The outcome is that they will mate more times as the sex ratio becomes more male-biased, without necessarily changing their receptivity to each mating (Figure 2; Table 1, criterion 1).

If convenience polyandry is not necessarily an appropriate conclusion to draw when females mate multiply without obvious benefits, when is it likely to occur, and how can we test it empirically (Table 1)? Changes in the female mating rate under different sex ratio regimes alone do not provide enough data to conclude that convenience polyandry is occurring, as discussed above. If, however, females accept a greater *proportion* of mating attempts when the sex ratio becomes more male–biased, a case can be made for convenience polyandry because this suggests that females alter their receptivity to mating based on the level of harassment they experience (criterion 1, Table 1).

The causes of convenience

Polyandry is convenient when resisting copulation is more costly than acceptance, and when females act to mitigate the costs of resistance by altering their propensity to mate. We emphasise that focusing on the costs of resistance is key to determining whether polyandry is convenient. If multiple mating has been selectively favoured to reduce resistance costs, then it is convenient under the usual definitions of convenience polyandry. If, on the other hand, polyandry evolves because it is otherwise beneficial (such that the costs of mating relative to resistance are reduced; Table 1, Figure 1) then it is not convenient in the sense implicit in the definition of convenience polyandry. In other words, it is not “true” convenience polyandry.

In many situations, we expect that females will act to reduce the costs of resistance. For example, females might gain protection from male mate guarding, which allows them to forage or oviposit uninterrupted. In other situations, male harassment might result in significant harm or even death, again making resistance not worthwhile (Box 1). However, if we consider that mating is not the only way that females can limit harm induced by harassing males, then to demonstrate convenience polyandry it is necessary to test if (and when) it is more costly for a female to resist a mating than it is to accept it (criterion 2; Table 1). Alternatives to acquiescing to mating can include crypsis and androgyny, as seen in damselflies [25-26] or hiding, as seen in water striders [27].

One method that has been used to test whether the costs of resistance (CR) exceed the costs of mating (CM; criterion 2) is by using ablation studies. In these studies, male genitalia are ablated so that they are unable to mate with females but can still harass them. If CR>CM then females housed with ablated males will suffer greater fitness costs than females housed with intact males. The ability to mate will allow females to mitigate the costs of resistance by accepting the (lower) costs of mating [36; see 60 for an elegant example of how female resistance can be manipulated without male ablation].

Despite the clear and intuitive nature of the ablation test, we know of no study that has shown the costs of resistance exceed the costs of mating (Table 1, criterion 2). Some of the apparent ambiguities from ablation studies (Table 1, criterion 2) might occur as a result of environmental effects on the costs of resistance and mating. For instance, environmental context might render polyandry convenient in some situations but otherwise beneficial in others. If, for example, the key cost of resistance is reduced foraging efficiency, we should compare females that have easy access to abundant food resources with those that do not when we wish to see if there is scope for convenience polyandry to reduce costs of resistance (criterion 3).

More generally, context is key to convenience. Before convenience polyandry can be tested, it is important to identify and measure the costs of mating in the absence of harassment in a variety of ecologically appropriate contexts [see 61-62]. The results of such studies can then be used to design experiments, including ablation studies, to measure the relative costs of mating and resistance (criterion 2), and how females respond to these in terms of their propensity to re-mate (criterion 3). Ultimately these results could inform experimental evolution studies that manipulate the environment to alter the relative costs of mating and resistance. Such studies would allow assessment of the selective potency of the benefits of mating vs the costs of resistance in driving evolutionary changes in the female mating rate (Table 1, criterion 3).

The consequences of convenience

Even when females do increase their receptivity to reduce the costs of resistance, polyandry might not remain convenient for long. When females engage in polyandry they might alter the other costs and benefits associated with mating in a number of ways, which we outline below. Importantly this can change whether polyandry is a matter of convenience, necessity or gain (Figure 1).

Indirect genetic benefits

Females can benefit from polyandry via the post-copulatory sexual selection that it elicits. By mating multiply, whether for convenience or not, females elicit sperm competition. As a result, their offspring are more likely to be sired by males that succeed in sperm competition, potentially resulting in indirect genetic benefits, including good genes [56] and Fisherian 'sexy sperm' for their sons [57]. Even if such benefits are weak [18; 20], they can reduce the costs of mating relative to resistance and could tip the balance, rendering polyandry more beneficial than it is convenient (Figure 1). It is, however, worth noting that indirect costs could also occur in this scenario through sexually antagonistic pleiotropy (i.e. polyandrous females producing high fitness sons and low fitness daughters) which may counterbalance these indirect benefits [63]).

Male harm

Another consequence of polyandry is that it induces sexual conflict over paternity, which can favour chemical or physical male traits that harm females, reducing their receptivity to future matings, and providing males with greater paternity certainty [24; 62]. This too will alter the relative costs of mating vs resistance, in this case increasing the costs of mating, which is expected to reduce the convenience of polyandry (Figure 1).

Coercive 'sexy sons'

Convenience polyandry is selectively advantageous because it acts to reduce the general costs associated with resistance (criterion 3) and as such females reduce their reluctance to mate with any male (criterion 4). However, when females engage in convenience polyandry, there is scope for sexual selection to arise through passive mate choice (i.e. there is no requirement for active discrimination between, and rejection of, several potential males). This could arise if females are more likely to mate with males that can impose larger costs, such as larger males. We call this Facultative Female Resistance (FFR, Table 1, Figure 1), to emphasise that female resistance can vary with the male they are interacting with, on a male-by-male basis. Importantly, by engaging in FFR, females can gain indirect genetic benefits through passive mate choice (i.e. good genes and/or sexy 'coercive' sons). These benefits then reduce the costs of mating compared to the costs of resistance and in turn shift the selection on polyandry away from convenience (although again see [63] for an example of a counter cost of polyandry in this context).

Water striders (Box 1) present a good example of how facultative female resistance can render convenience polyandry beneficial in other ways, making it no longer strictly about reducing the costs of resistance. In many species of water strider, males have non-intromittent genital claspers that allow them to endure female struggles [28]. The larger these claspers, the better able males are to overcome such struggles and successfully mate. Importantly, however, the size of these structures is heritable [41], which means that by reducing their reluctance to mate with males with large claspers, females can produce "sexy sons" that in turn will have higher mating success (see Table 1, criterion 4).

Strategic ejaculate allocation

Perhaps most importantly, polyandry can induce positive feedback loops that lead to its persistence despite non-negligible costs of mating [21; see Figure 1]. Such positive feedback occurs because polyandry can result in sexual selection for smaller ejaculates in males, reflecting the trade-off between partitioning ejaculates across many matings versus increasing success in sperm competition over a few matings [64-67]. When males either control mating or when polyandry is convenient, the variance in the number of mates for a given female will increase. Under these conditions, males will benefit from bet-hedging – spreading the risk of failing to sire any offspring by investing more in mating with many females and transferring smaller ejaculates to each of them [65-67].

Bocedi & Reid [21] modelled this scenario and found that such strategic ejaculate allocation increases the risk of sperm limitation for females and results in selection on increased female mating frequency, even when mating is costly to females. These feedback loops were particularly potent, with a higher likelihood of evolving polyandry, when sperm precedence was strong. When sperm precedence is strong, a single male (usually the first or the last) will sire the majority of a female's offspring. Under these conditions, investing in large, expensive ejaculates is far riskier than investing in many smaller ejaculates because the likelihood of siring any offspring from a given mating is lower than when sperm are mixed. Under strong sperm precedence, selection will favour smaller ejaculates and subsequently increases female mating rates to prevent sperm limitation. Empirical evidence for the predictions of these models has been found, most notably across the bushcrickets (Orthoptera: Tettigoniidae), where males in more polyandrous species have larger testes but transfer smaller ejaculates to increase their relative paternity success across matings [68-69, see also 70 for an excellent example of a bespoke model and an empirical test of strategic ejaculate allocation theory].

Many of the processes outlined above will increase the optimal mating rate for females by increasing the benefits of mating. In particular, if the risk of sperm limitation is non-negligible, then polyandry becomes a matter of necessity rather than convenience (Figure 1). The opportunity for these feedback loops to occur leads us to suggest that true convenience polyandry might be a rather fleeting phenomenon, because the consequences of polyandry (in terms of sexual conflict and pre- and post-copulatory sexual selection) will almost always change the relative costs of mating, and so polyandry may become advantageous independently of the costs of resisting. Importantly, we are not suggesting that we no longer expect females to attempt to reject some or all males, or that resistance to male harassment is no longer an important component of how mating behaviour evolves. Rather, we wish to emphasise that selection on polyandry just to reduce mating costs – the essence of convenience polyandry – may typically be only a transitory phase in the overall evolutionary origin and maintenance of polyandry.

Concluding Remarks

Convenience polyandry requires that the costs of resistance exceed the costs of mating, for instance when male density is high or when males coerce females. It also requires that females alter their receptivity to mating in order to mitigate the costs of resistance and not to gain other benefits. Whether polyandry can be considered convenient depends on whether selection favours polyandry because it mitigates a cost (resistance) or because it is otherwise beneficial. Some may argue that this is purely semantic, but to understand closely associated evolutionary processes (such as convenience vs benefits-driven polyandry) it is crucial to determine exactly how selection acts and what it acts upon. Convenience polyandry – as generally accepted – serves to reduce the costs of resistance, but once polyandry starts it can induce other costs and benefits associated with mating such that it is no longer a matter of convenience (Figure 1). As such, convenience polyandry may be a fleeting phenomenon, but it could also be a phenomenon with the power to shape mating systems and patterns of sexual selection (Box 3).

Polyandry may be a matter of convenience under some situations, but within species and populations selection for polyandry may differ according to the environment, female state, and the male’s ability to overcome reluctance (see Box 3). To understand the evolutionary significance of cost mitigation in driving female mating behaviour, researchers must explicitly test the convenience polyandry hypothesis, all the while maintaining an awareness of potential socio-cultural biases about whether or not we implicitly expect females to be monandrous or polyandrous (Box 2)

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Glossary

Benefits driven polyandry: when females mate multiple times in order to gain direct fitness benefits for themselves or indirect benefits that improve the fitness of their offspring.

Convenience polyandry: when females mate more times than they need to achieve full fertility because resisting extra mating attempts is more costly than acceptance.

Cost mitigation: any mechanism that serves to reduce loss of fitness caused by an extrinsic stressor.

Costs of resistance (CR): fitness costs incurred by one sex as a result of attempting to resist or avoid copulation.

Costs of mating (CM): fitness costs incurred by one sex as a result of copulation.

Direct benefits: when polyandry increases female longevity or fecundity, for instance through nuptial gifts or ejaculate components.

Facultative female resistance (FFR): when females preferentially mate with males that impose higher costs of resistance (CR), i.e. that are more coercive.

Fisherian benefits: when females gain a fitness benefit from mating multiply ('sexy sperm') or with certain males ('sexy sons') because their sons are endowed with their fathers superior competitive abilities under sexual selection.

Indirect benefits: when polyandry provides females with genetic benefits for their offspring by improving offspring survival, fecundity and mating/fertilisation success.

Null polyandry: when female multiple mating serves to prevent reproductive failure.

Mate-guarding: after copulating one sex (usually the male) remains associated with their partner to reduce the likelihood that they will mate again.

Monandry: when females only mate once (strict monandry) or mate multiple times with the same male (social monandry).

Polyandry: when females mate multiple times with multiple males.

Reproductive failure: when an individual fails to produce viable offspring either because they fail to mate entirely, do not copulate with a compatible individual, or do not receive or pass sperm during copulation.

Sexual harassment: when an individual of one sex attempts to mate with a non-receptive individual of the opposite sex.

Sex-role reversal: a rare mating system characterised by paternal care, male choice and competition between females over access to males. Commonly cited examples include several species of pipefish and seahorse, wading birds such as phalaropes and jacanas, and dendrobatid frogs.

Sexual receptivity: likelihood of an individual accepting a given mating attempt.

Sexual coercion: when an individual of one sex uses force or intimidation to copulate with an individual of the opposite sex.

Sexual conflict: when the fitness optima for a trait differs between the sexes.

Superfluous mating: a mating that does not increase fertility or fitness.

Unconscious or implicit bias: beliefs about certain groups or concepts that individuals are unaware that they possess.

Figure legends

Figure 1. How selection operates on the female mating rate under convenience polyandry, benefits-driven polyandry, and null polyandry. Separating the costs of

resistance (CR) from the costs of mating (CM) is crucial to understanding whether polyandry is convenient. If CR and CM are grouped together then the forces that select for polyandry (convenience vs benefits vs mating failure) are obscured. In this figure we show how different forms of polyandry can result in selective feedback loops between sexually selected male traits (grey boxes) and the female mating rate. For instance, convenience polyandry and null polyandry generate selection on males that may facilitate benefits-driven polyandry. Likewise, if strategic ejaculate allocation renders females sperm depleted, there will be positive selection on the female mating rate (to reduce MF). These feedback loops suggest that true convenience polyandry is unlikely to persist for long, given the opportunities for other forms of selection that it generates.

Figure 2. Distinguishing convenience polyandry and null polyandry [33]. Shown are the predicted *number* of matings (A – solid lines) and *proportion* of mating attempts accepted (B – dashed lines), when harassment (or encounters with males) varies. Null polyandry (blue) occurs when females are equally receptive to each mating attempt, and convenience polyandry (red) occurs when females change their receptivity to mating according to the costs of resistance. These two cases are all but indistinguishable with regards to mating *number*. When the *proportion* of mating attempts accepted is considered however, we see that null polyandry (blue dashed lines) does not change with the level of harassment, while for convenience polyandry (red dashed lines) the proportion accepted increases.

Figure I. Water strider (image credit Locke Rowe)

Box 1. A convenient case study – the water striders.

The water striders (Gerridae) (Figure I) are one group where the importance of convenience polyandry (CP) has been empirically demonstrated [28]. The work conducted in this family serves as a gold standard for understanding the importance of cost mitigation for female mating rates. Yet these studies also show the complexity of convenience polyandry, including the specific environmental conditions required for it to occur, and the roles of female condition and mate choice. Below we outline the work that has been done in the Gerridae, using the framework we propose in Table 1 as a template.

In the Gerridae, females alter the proportion of matings they accept (criterion 1) according the level of harassment they experience (the operational sex ratio; OSR [28]). Mating is not without its costs for female water striders, and so they are often reluctant to mate, which results in pre-mating struggles. These struggles (i) prevent females from foraging efficiently and (ii) attract predators [28-29]. When females permit copulation these costs are lowered because in some species females can (i) forage efficiently whilst in copula. Predation risk (ii) is also lower when copulating rather than struggling as the water surface is less agitated. The costs of mating vs resistance are highly context dependent however, such that when females are satiated or predation risk is removed mating is more costly than resistance (CM>CR, criterion 2). Females respond to these context dependent costs, engaging in higher levels of polyandry when it is convenient and resisting superfluous matings when it is not (criterion 3; [28]). The story becomes even more complex when we consider facultative female reluctance (FFR; criterion 4), which occurs for instance in the water strider *Aquarius remigis.* In *A. remigis*, females mate preferentially with large males [30], but this only occurs when the costs of resistance are low compared to the costs of mating (i.e. under low male density or when females are satiated; [28]). When male density is high or females are hungry, convenience polyandry takes over - the costs of resistance exceed the costs of mating with males regardless of size, and females mate indiscriminately (criterion 4).

Box 2. Preconceptions about polyandry

In the sexual selection and sexual conflict literature, lingering historical preconceptions about how females (including women) should behave have been repeatedly suggested to colour our interpretations of male and female mating behaviour in the absence of theoretically sound reasoning [45-46]. Societal norms may be projected onto study species, with the sexes described using different language even when the same behaviour is being studied. The role of socio-cultural biases is perhaps most apparent in the case of sexual cannibalism, where loaded terms with highly negative connotations (such as “rapacious”, “voracious”; 48) are used to describe females that behave in ways that are not in-line with societal expectations.

Polyandry may represent another area where socio-cultural unconscious biases have influenced interpretations of female mating behaviour (45). The lack of thorough theoretical and empirical scrutiny that the convenience polyandry hypothesis has received, which contrasts markedly with the benefits-driven and bet-hedging approaches [16-22], leads us to question why convenience is commonly described as an explanation for female multiple mating. We suggest that socio-normative biases about female behaviour may contribute to this pattern. When polyandry arises through selection on males, as is the case for convenience polyandry, it fits with societal expectations exemplifying the stereotype of the coy female responding to the evolutionary demands of males: females only mate multiply to curtail the costs imposed upon them by males.

Table 1. Framework for establishing whether polyandry is convenient[al]

	Criterion	Rationale	Examples	Refs
1	Females accept a higher proportion of mating attempts by males	As harassment costs increase (i.e. the sex ratio becomes more male-biased), females accept a greater proportion of mating attempts. If only the absolute number of matings is shown to increase it is not possible to distinguish between "null" polyandry and convenience polyandry (Figure 2). If females increase the proportion of mating attempts they accept, then a case can be made for convenience polyandry, because this suggests that females alter their propensity to mate based on the costs of resistance.	The number of matings a female engages in increases with the sex ratio in the butterfly *Bicyclus anynana.* There are no data regarding the proportion of mating attempts that females accepted and so it is not possible to confirm convenience polyandry in this case.	[21,25,71]
2	The costs of resisting or avoiding (CR) a mating exceed the costs of mating (CM)	Convenience polyandry cannot be assumed when females mate multiply without gaining any perceptible benefit. To demonstrate that convenience polyandry *may* be operating requires that CR exceed CM, i.e. resistance to mating must be shown to carry greater fitness costs than acceptance.	CR>CM can be tested using ablation studies, whereby females are maintained with males that have intact or ablated genitalia. If CR > CM females maintained with ablated males will have lower fitness than those kept with intact males that can mate. Many ablation studies are not conducted under relevant ecological conditions and overlook key factors that make polyandry convenient (i.e. starvation, predation risk, Figure 1 and Box 1).	[43, 52]
3	Females alter their propensity to mate according to changes in the costs of resistance (CR)	Testing CR>CM is not always straightforward as context is often key. Moreover, when benefits of polyandry accrue, CM necessarily decreases meaning that CR may be relatively high without polyandry being convenient. Therefore, it is necessary to show not only that CR>CM (criterion 2) but that females alter their propensity to mate according to changes in CR. Selection acts on the female mating rate through different channels when polyandry is convenient (reducing CR) compared to when it is otherwise beneficial (reducing CM; see Figure 1).	CR may not always exceed CM (see Box 1) and so ablation studies can yield contrasting results. The seed beetle, *Callosobruchus maculatus* offers a case study - females have been suggested to benefit from accepting superfluous matings because mate-guarding reduces interruptions during oviposition. However, ablation studies do not support this assertion. This may be because mating is beneficial (CM drops) when females are dehydrated, as ejaculates are water rich. In order to test whether females respond to elevated CR (as opposed to reduced CM) in this species the benefits of mating must be removed (i.e. females should be hydrated). There are many other reported cases where female state can reduce CM, and so context-dependent benefits should be considered when designing ablation studies.	[53-57]
4	Females mate indiscriminately with respect to male phenotype	When polyandry is convenient the benefits that females gain come from reducing CR not CM. As such, under convenience polyandry the benefits of accepting only preferred males are superseded by the importance of mitigating the overall costs of resistance. Cost mitigation can also influence mate choice though because individual males vary in how costly they are to resist. Females may facultatively assess these costs of resistance and alter their reluctance to mate. While this appears to fit with the definition of convenience polyandry, facultative female reluctance (FFR) can confer indirect benefits to polyandrous females.	Many examples exist where cost mitigation and mate choice are linked. For instance, females might mate preferentially with large males or males with large grasping apparatus. Examples such as these have sometimes been taken to suggest that the costs of resistance influence female mating decisions. The water striders (Box 1) offer a particularly good example of how these processes differ but can interact.	[58-59; 62]

[a]In this Table we list the criteria that must be fulfilled to establish whether females mate multiply due to convenience polyandry, we explain our rationale, and we provide examples and methods to test each criterion.

Figure 1 revised

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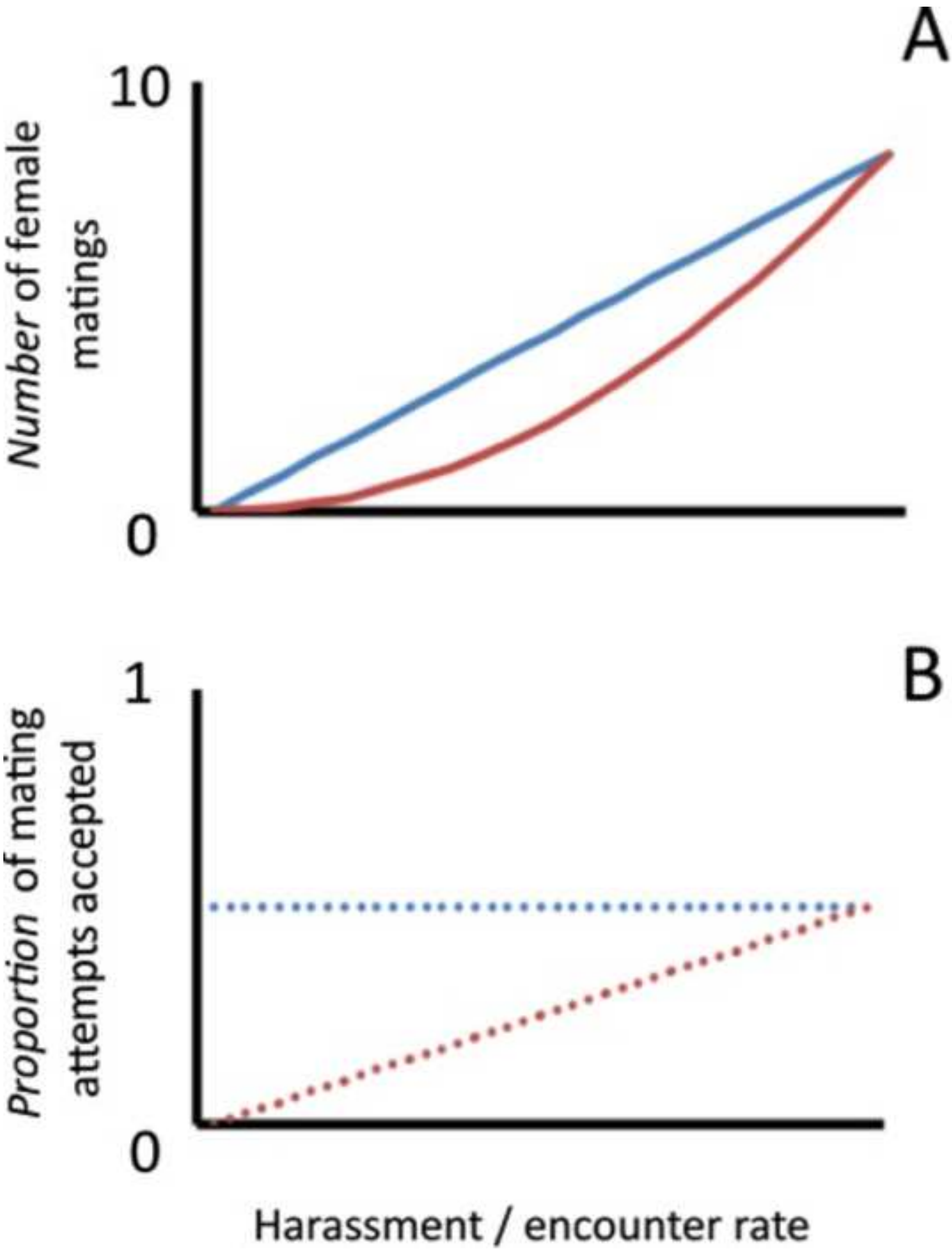
A
10
0
Number of female matings
B
1
0
Proportion of mating attempts accepted
Harassment / encounter rate

Box 1, Figure I

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WS copulation for Box 1.jpg

Outstanding questions

- Do existing examples of apparent convenience polyandry hold up to more rigorous testing under the framework that we propose?
- How common is convenience polyandry compared to benefits-driven polyandry?
- Direct and indirect benefits explanations for polyandry have been subject to considerable empirical and theoretical scrutiny – how does convenience polyandry compare when subject to similar assessment?
- Can/does convenience polyandry result in feedback loops that render multiple mating beneficial or necessary (rather than simply convenient)?
- Can polyandry evolve from a strictly monandrous state due to convenience?
- How has the social and historical context of sexual selection research influenced the way that we view and interpret polyandry?