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Polyandry: the history of a revolution

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We give a historic overview and critical perspective of polyandry in the context of sexual selection. Early approaches tended to obfuscate the fact that the total matings (copulations) by the two sexes is equal, neglecting female interests and that females often mate with (or receive ejaculates from) more than one male (polyandry). In recent years, we have gained much more insight into adaptive reasons for polyandry, particularly from the female perspective. However, costs and benefits of multiple mating are unlikely to be equal for males and females. These must be assessed for each partner at each potential mating between male i and female j, and will often be highly asymmetric. Interests of i and j may be in conflict, with (typically, ultimately because of primordial sex differences) i benefitting and j losing from mating, although theoretically the reverse can also obtain. Polyandry reduces the sex difference in Bateman gradients, and the probability of sexual conflict over mating by: (i) reducing the potential expected value of each mating to males in inverse proportion to the number of mates per female per clutch, and also often by (ii) increasing ejaculate costs through increased sperm allocation. It can nevertheless create conflict over fertilization and increase conflict over parental investment. The observed mean mating frequency for the population (and hence the degree of polyandry) is likely, at least in part, to reflect a resolution of sexual conflict. Immense diversity exists across and within taxa in the extent of polyandry, and views on its significance have changed radically, as we illustrate using avian polyandry as a case study. Despite recent criticisms, the contribution of the early pioneers of sexual selection, Darwin and Bateman, remains generally valid, and should not, therefore, be negated; as with much in science, pioneering advances are more often amplified and refined, rather than replaced with entirely new paradigms.

1. Introduction

That the males of all mammals eagerly pursue the females is notorious to every one. So it is with birds; but many male birds do not so much pursue the female, as display their plumage ... With the few fish which have been observed, the male seems much more eager than the female; and so it is with alligators, and apparently with Batrachians .... The female, on the other hand, with the rarest exception, is less eager than the male ... she is coy, and may often be seen endeavouring for a long time to escape from the male. ... We are naturally led to enquire why the male in so many and such widely distinct classes has been rendered more eager than the female, such that he searches for her and plays the more active part in courtship.

Darwin [1, vol. I, pp. 272–273]

It is thus desirable to search for a fundamental cause of intra-masculine selection .... This cause should show us why it is a general law that the male is eager for any female, without discrimination, whereas the female chooses the male. ... Experiments with *Drosophila melanogaster* ... show that the contribution of males to the next generation is much more variable than that of females. ... Males must therefore be inherently subject to stronger selection than females, which must be due to a more intense intra-sexual action. The intensity of intra-masculine selection is due to the greater dependency of males on the frequency of insemination. This seems to be inherent in primary differentiation in both animal and plants. ... Undiscriminating eagerness in males and discriminating passivity in females must have been early effects of intra-masculine selection and are naturally widespread.

Bateman [2]

Hogamus, Higamus men are polygamous,
Higamus, Hogamus, women monogamous.
  Credited to various authors during the past century (see http://quoteinvestigator. com/2012/03/28/hogamous/)

These quotations show that a difference in male and female sexual behaviour is not only a common expectation in Western culture, but a prediction of the two seminal writers on sexual selection: Darwin [1], who first proposed the concept, and Bateman [2] who provided the first rigorous explanation for its action through the primary sexual differentiation owing to anisogamy. Since the 1970s, the era of the 'behavioural ecology revolution' [3,4], sexual selection expanded to become one of the biggest research fields in evolutionary biology, and continues to be so. A. R. Wallace's views on sexual selection through female choice appear to have been largely ignored, but the modern concept of honest advertisement in mate choice appears essentially to be a reiteration of Wallace's ideas [5].

Speculation currently abounds as to what extent the popular Western view of males and females itself generated the expectations for male and female sexual behaviour for Darwin and Bateman, and whether this has contributed to a bias in the collection and interpretation of evidence. Dewsbury [6] presents a thoughtful critique of what he calls the 'Darwin–Bateman paradigm' (henceforth DBP), defined by three predictions: (i) male reproductive success varies more than that of females, (ii) male reproductive success increases more from multiple matings than does that of females, and (iii) males are characteristically eager to mate and relatively indiscriminate, and females more discriminating and less eager. He concludes that sex stereotypes appear to have influenced these conceptions, and while acknowledging the heuristic value of the paradigm, calls for further empirical investigation to elucidate the many exceptions. We would also add as part of DBP: (iv) the assumption that these predictions are generated ultimately by anisogamy—something that has been attacked recently in the so-called 'gender-neutral' models of sexual selection ([7]; but see [8]). Roughgarden [9] and Roughgarden et al. [10] have suggested that the entire concept of Darwinian sexual selection is fundamentally flawed, and propose an alternative viewpoint based on social cooperation, a suggestion which attracted an intense collective and convincing rebuttal (see the multiple responses in Science, 2006, vol. 312, 689–694). Prior to Roughgarden's proposals there had already been extensive consideration of sexual cooperation (such as biparental care in socially monogamous birds, which nevertheless involves sexual conflict; [11]), so her proposition that the whole of sexual selection theory needs replacement is remarkable; the fits between prediction and evidence (for instance, in sex allocation, [12]; competitive mate searching, [13]; and many other areas, [14]) represent triumphs for the theory of sexual selection as great as for any aspect of natural selection. Plausible views on sexual selection as a subset of social selection stem from West-Eberhard [15,16] (also see [17] and [18]), and the call by Pizzari & Gardner [19] for more integration of inclusive fitness into sexual selection studies seems well justified.

It is important to separate what Darwin [1] wrote about differences between the sexes in humans in terms of behaviour and achievement, from the general aspects of DBP as listed in (i)–(iv) earlier. Darwin's views on human sex differences were probably not only constrained by the cultural ethos of Victorian England that subordinated women and denied them opportunities for achievement, but also by his lack of knowledge of genetic mechanisms. For example, to support a theoretical claim that men are more intelligent than women because of the higher intra-sexual selection on males, one would need to know why an autosomal mutant gene for increased intelligence would become sex limited to males; i.e. why such a gene would be costly when expressed in women?

However, putting aside this aspect of Darwin's writing on sexual selection, here, we argue that there is no reason to reject predictions (i)–(iii) of DBP, and strongly support the defence of anisogamy as the primary cause of the difference in sex roles by Schärer et al. [8], i.e. DBP assumption (iv).

There have been many claims that sexual selection studies have been misleadingly biased owing to gender stereotypy [6,7,20–24], and more recently this view has been extended to sexual conflict [25], a proposal strongly contested ([26], with a response [27]). It is hard to deny that an imbalance in perspective resulted from the early focus on males, but what is less certain is that this led to misconceptions rather than simply researchers focusing initially on males, and later on females. Thus, if one asks whether cultural stereotypes influenced the DBP and the subsequent development of sexual selection and sexual conflict, the answer might well be that they have. If one asks whether their influence negates current orthodoxy, we believe that the answer would be that it has not. Setting aside Darwin's views on human gender differences, across the animal kingdom as a whole, and despite many exceptions related to sex-role reversal and other phenomena [28], both the weight of current evidence and theoretical expectation greatly supports the generality of DBP. Though its initial acceptability may have been increased by gender stereotypes [6], it is even possible that social enlightenment and the rise of Western feminism now make DBP less acceptable. Further, although cultural stereotypes sometimes generate incorrect reflections of underlying biology, this is not always the case. Whatever their influence, the important issue is whether DBP is, or is not, scientifically valid in general for animals in which males have typically low parental investment (PI) sensu Trivers [29] relative to females, i.e. for most animals. Our view is that, even though there are many exceptions, in this general sense, DBP remains logically correct.

Owing ultimately to anisogamy, DBP asserts that male fitness generally increases steeply with number of matings with different females and gives a major reason why males should mate multiply and opportunistically. But, why should females mate with several males? In recent years there has been a vast amount of literature on the potential benefits of multiple mating to females, with increasing evidence that in some cases the benefits can be substantial (reviewed by Jennions & Petrie [30] and Simmons [31]). In table 1, we summarize some of the commonest proposals for the costs and benefits of multiple mating by each sex. The literature distinguishes between 'direct' benefits (such as resources which increase survival or reproductive success of an individual or its offspring, discounting any genetic effects), and 'indirect' benefits (where the benefits of mate choice relate to the quality of the genes in the chosen mate).

Thus there has undoubtedly been a major and important shift in how we view female sexual behaviour and polyandry: while most work prior to around 1980 tended to ignore female interests, there is now a much greater focus on the female viewpoint in both pre- and post-copulatory aspects of mate choice, and the adaptive function of female behaviour and morphology [18,30,32–36]. This is a related

Table 1. Some commonly proposed costs and benefits of multiple mating.

sex	benefits	costs
male	Darwin–Bateman effect—male fitness increases steeply with number of matings with different females due ultimately to anisogamy	ejaculate expenditure, plus any subsequent paternal care
		increased risks (e.g. predation, disease) during courtships, copulations, etc.
		increased time or energetic costs owing to courtship, mating, mate-guarding, etc.
female	increased proportion of eggs fertilized as sperm numbers increase	increased risks (e.g. predation, disease) during courtships, copulations, etc.
	insurance against a prior mate being sterile	increased time or energetic costs
	increased number of offspring produced	increased harassment or other costs of male–male competition
	increased genetic diversity of offspring	
	permits post-copulatory mate choice	
	reduced cost of male coercion: persistence and harassment	
	paternity confusion—protection against infanticide	

but different issue from that of the general validity of DBP. We argue here that neither this revolution in our understanding of polyandry from the female perspective, nor the issues of sexual stereotypy, is a reason to reject the generality of DBP.

We refer here to polyandry in the sense of multiple mating (or more strictly, multiple ejaculates), i.e. a female copulates with and is inseminated by more than one male for fertilization of a given clutch or litter of progeny. Although seldom stressed explicitly, DBP relies on 'polyandry' meaning 'receiving more than one ejaculate' for fertilization. *A priori*, polyandry in the sense of sequential monogamy without any ejaculate overlap yields the same expected benefit for a female to achieve her single sequential mating per clutch as the expected benefit of each mating to a male. Our use of polyandry as multiple mating by the female makes no comment about male behaviour, which we generally assume to copulate opportunistically (promiscuously). This use differs from the use of the term polyandry by Shuster & Wade [37, p. 162], who give much more specific definitions for mating patterns related to the variance in mate numbers of each sex.

Our aim in the present review is to give a historic overview of polyandry (multiple mating) in the context of sexual selection and sexual conflict, and to give a critical perspective of current views in this field. We support the generality of DBP and suggest that indirect measures of the intensity of sexual selection are more robust than recently claimed. We show how polyandry reduces the benefits of matings to males, and discuss how sexual conflict over individual mating decisions summates to give the population level of polyandry. To illustrate how views of polyandry have changed, we outline the history of polyandry research in birds as a case study.

2. Bateman's principles

Bateman's [2] conclusions have been criticized on experimental and technical grounds [38], or on the grounds that the difference in variance in reproductive success between the sexes can be attributed to purely random processes [39,40], or for other reasons does not reflect the intensity of sexual selection [41,42]. In re-analyses of Bateman's data, both Arnold & Duvall [43] and Snyder & Gowaty [38] concluded that in his experiments, female reproductive success also increases with number of mates (a finding that is now proving commonplace, see [31]), and that number of mates also explains a significant amount of variation in female reproductive success. Wade & Schuster [44,45] nevertheless argue that there is actually little reason to negate Bateman's experimental work on these grounds. However, a recent repetition of his experiments now suggests flaws owing to his methods of assigning paternity [46]. The situation is rather reminiscent of Mendel, because despite these controversies concerning his experiments, the generality of Bateman's seminal conclusion still appears robust. His crucial point, as Trivers [29] was first to stress, is that in species where females invest a great deal more in progeny than males, female reproductive success is likely to increase much less steeply than male reproductive success with number of matings after the first.

Sutherland [39] has plausibly been claimed that the observed difference in variance in reproductive success between the sexes noted by Bateman could have arisen by random search processes, given the constraints on the two sexes. However, as Schärer *et al.* [8] point out, Sutherland's suggestion was not that variance in mating success arises purely by chance, but that under random mating the difference between the sexes in the time taken to find a mate (due ultimately to anisogamy) could produce this variance by random processes. Sutherland [39] stated this quite clearly:

> I simply wish to make it clear that random mating can produce variance in mating success and this variance will be greater for the sex with the shorter mating time. . . . My point is simply that variance in mating success does not, by itself, provide evidence for the existence of sexual selection.

Sutherland's 'mating time' is the time invested in a given mating, or in replenishing gametes, and/or in parental care. It is the 'time out' out of the mating pool, during which an individual cannot search or otherwise compete for further matings, as opposed to 'time in', during which an individual

competes for mates (*sensu* Clutton-Brock & Parker [47]; see also [40]). Greater variance in reproductive success will indeed arise through random processes in the sex with the shorter time out: this should not be seen as direct evidence for sexual selection, but rather as evidence for its potential [48,49]. All else being equal, a mutant male that achieves twice the number of matings as wild-type males would have a huge sexual selective advantage, invading at twice the rate, whereas a mutant female with twice the number of matings per cycle would not. The slopes of the regressions of fitness against number of matings (known as the 'Bateman gradients') are the key measures. The relative variances simply give (at best) a measure of the opportunity for this form of selection through the number of matings. Variance in male fitness has thus been proposed as a useful measure of the 'opportunity for sexual selection' on males [50,51], commonly now termed I_{mates}, see also [37,52,53], based on Crow's [54] proposal that the opportunity for selection is proportional to the variance in fitness divided by the square of mean fitness.

Many alternative ways of estimating the intensity of sexual selection have been proposed, and the issue remains highly controversial [37,42,48,49,55]; the 'opportunity for sexual selection' can be highly dependent on the details of the biology of a given species [56] and may not be equivalent to its intensity [42]. Following Darwin and Bateman, Trivers [29] proposed relative PI as a measure of the intensity of sexual selection, followed by Emlen & Oring [57] who proposed the operational sex ratio (OSR; the relative number of males and females immediately available to mate in a given locality), followed by Clutton-Brock & Vincent's [58] suggestion of potential reproductive rates (PRR; the potential rate at which a given sex can produce offspring if unlimited by mating with the opposite sex). Furthermore, measures have been (and continue to be) proposed [37,42]. However, such general ('indirect') measures of sexual selection can be problematic [42], and the actual intensity may depend on the exact conditions operating in a given system, such as mortality schedules, the potential for mate-guarding and monopolization, the variances in mate quality and the operation of mate choice, the mode of fertilization, etc. Indeed, the need to measure precisely the intensity of sexual selection at all has been eloquently questioned by Grafen [59] (see also [42]) on the grounds that the interesting aspect of sexual selection is in studying (as Darwin did) exactly how it has shaped adaptations, rather than measuring its strength.

The seminal paper of Klug *et al.* [42] attacked the use of indirect measures such as OSR, I_{mates}, PPR, and the Bateman gradient (which are closely correlated under male-biased OSR), claiming that in order to reflect the intensity of sexual selection they require very restricted conditions (notably very strong mate monopolization), and seriously question the validity of conclusions based on these measures. They reviewed empirical studies where direct selection gradients were calculated with respect to a phenotypic trait, and whether there was congruence between direct selection and the patterns suggested by I_{mates}. This comparison showed only limited success, and they argue that less emphasis should be placed on indirect measures in favour of measuring selection directly on phenotypic traits. For instance, if (say) male horn size is hypothesized to have evolved through intra-sexual selection, it is more useful to measure the reproductive success of males differing in horn size than OSR.

We applaud the call by Klug *et al.* [42] for the use of direct rather than indirect measures. This appears desirable when possible, e.g. for within-species studies, but will often be unachievable for comparative studies. Estimates of indirect measures such as OSR or PRR are usually much more accessible. However, we disagree with Klug *et al*'s claim that indirect measures are restricted in their usefulness (see also [48]). In their analysis, it is unsurprising (as they point out) that indirect measures do not correlate with sexual selection differential when there is (i) no genetic variance, or (ii) where, as in their model, the selective benefits of trait values remain constant, because increasing OSR simply increases the sample size from which male parents are drawn each generation. The case for indirect measures relies on the biological likelihood that positive correlations between selection and OSR are commonly generated.

A general problem with their model is that it does not allow for the effect of the expected inverse relationship between OSR and male time out (high OSR is likely to occur when males have low times out, i.e. high PRR). Thus, in a continuously breeding population at steady state, at low OSR, a male with a given high trait value gains matings more quickly when in the mating pool, but spends a higher proportion of his total reproductive life on time out than average males. By contrast, at very high OSR (and hence trivially low male time out), males return to the mating pool almost immediately and their gain rate is limited mainly by the availability of females. To give a simple example, suppose one female per adult male becomes available every 4 time units. Consider a mutant male that gains matings at twice the rate of wild-type males (e.g. by searching twice as fast). Imagine a low OSR population, where the male time out is 3 units and where it takes wild-type males an average of 1 time unit to find a female; it, therefore, takes the mutant male only 0.5 units. The selective (i.e. mating rate) differential of the mutant is $1/3.5 - 1/4 = 0.036$. Now imagine a higher OSR population where male time out is just 1 unit. It now takes wild-type males on average 3 time units to find a female, and the mutant takes 1.5 units. The mating rate difference is now $1/2.5 - 1/4 = 0.15$. This effect alone is sufficient to generate a high positive correlation between selection on the fixed trait value and OSR (see Note added in proof).

Setting this basic problem aside, several specific features can also contribute to the desired positive correlation. We note that when females choose males by a fixed threshold criterion across the population, Klug *et al.* [42] found a good correlation between selection differential and both OSR and I_{mates}. In the case of 'best of N' choice, they found no obvious correlation; here, females must accept a mating even if most of the males have low trait values. If females could leave such groups without mating, and move to groups containing males with higher trait values, a positive correlation between selection and OSR might be generated. Similarly, if female choice and male−male competition favour the same male trait values, e.g. due to male−male competition, then the desired correlation might again be expected. Where males fight for leks or breeding territories, these sites are likely to become controlled by males with high combat (and hence also choice) trait values ('resource structuring' [60]). Further, Klug *et al.* only considered cases where females mate once (i.e. they excluded post-copulatory sexual selection). However, the sperm competition level may increase with OSR. Post-copulatory male traits that are sexually selected (e.g.

more available sperm, more competitive sperm, better mating plugs, more effective male-induced female unreceptivity after mating, etc.), may be increasingly favoured as OSR (and sperm competition) increases. Thus, even without including the negative relation between male time out and OSR, we would often expect the selective differential across a given male trait range to become steeper as OSR increases.

Finally, rather than using the fixed additive genetic variance approach of Klug et al., it can be argued that what is more important is the optimal deviation—e.g. how much a male trait will deviate from that of the female through sexual selection. As male–male competition increases, the range of favourable mutants will often increase. If winning a mating opportunity depends on the relative arms levels of the combatants, evolutionarily stable strategy (ESS) models show that armament increases with the number of males competing in each combat for access to a female [61]. Provided that relative advantage increases with male–male competition, this phenotypic approach typically generates positive correlations between optimal expenditure (here armament) and OSR.

Thus, while direct measures are better for empirical studies, indirect measures should be treated cautiously but not discarded; they will usually be required to interpret the range of diverse adaptations across populations, and remain useful for comparative analyses. Use of multiple measures when possible seems amply justified [42]. Indirect measures remain invaluable for theoretical studies.

Although many counter examples can be proposed, DBP still remains valid for the majority of species with internal fertilization and zero or low male parental care. Natural or experimental manipulations within a species often offer the best evidence. For instance, naturally occurring environmental changes in sex ratio resulted in sex-role reversal associated with a change in ordering of relative PI in zaprochiline bush crickets [62], and artificially manipulated changes in sex ratio reversed Bateman gradients in the predicted manner in the sex-role reversed pipefish, Syngnathus typhle [63].

3. Polyandry and Bateman gradients

Bateman's work preceded current interests in polyandry and post-copulatory aspects of sexual selection that have become prominent in recent years [64]. In our view, probably the biggest threat to Bateman's principles comes from the effect of polyandry, which acts to reduce the value of each mating to a male for the following reasons:

(a) Economic costs of sperm

Bateman has often been criticized for his assumption that sperm are cheap and unlimited; the costs of each ejaculate are generally non-trivial [65–67]. Under post-copulatory sexual selection, the cost of a given ejaculate to a male may vary immensely. Sperm competition increases ejaculate costs to males (reviewed in [68]), and this will reduce the male Bateman gradient [64], maximally when sperm competition follows a fair raffle (sensu Parker & Pizzari [68]). For example, under intense sperm competition, such as found in broadcast spawning marine invertebrates, male and female body and gonad sizes are typically equal [69], and hence, despite anisogamy, the costs of the gametes expelled at reproduction are probably similar for the two sexes.

(b) Costs of promiscuity

If a male increases his risk of losing fertilizations with a female by leaving her to search for further matings (e.g. by not guarding), this can select against male promiscuity in the sense of male departure for further mate searching [44]: female promiscuity can limit male promiscuity through risks of lost paternity.

(c) Shared gains per mating

It is not often pointed out that polyandry, where the female mates on average n times per clutch, reduces the expected benefit of each additional mating for a male (i.e. the male Bateman gradient): in the simplest case the reduction (and the difference between the male and female Bateman gradients) is by a factor of $1/n$, because n males compete for the same progeny. We illustrate the logic of this effect in box 1 using a simple linear benefit model in which we consider the extra fitness gained by a rare mutant male and female that achieve on average one additional mating more than wild-type individuals (table 2). To keep the model simple, we assume an adult sex ratio of unity: thus the male Bateman gradient arises as a result of each adult wild-type male donating an ejaculate to n different females for each female clutch produced, whereas the female gradient arises from each adult wild-type female receiving ejaculates from n different males for each clutch she produces. We also assume that extra matings can increase the number or viability of offspring in a clutch (e.g. via nuptial gifts). The model in box 1 shows that this reduction in the Bateman gradient owing to polyandry is independent of the mechanism of sperm competition, but is dependent on the way that the male mutant gains his extra mating (by outcompeting rival males for the fixed number of matings, or by coercing a female into an extra mating). It also shows that although polyandry reduces the difference between the male and female Bateman gradients, it does not alter which is greater.

This effect of polyandry has interesting implications, including a potential reduction in sexual conflict over mating. It can nevertheless potentially create conflict over fertilization, and increase sexual conflict over PI. Shuster & Wade [37] and Pizzari & Bonduriansky [70] also discuss implications of sperm competition for Bateman's principle, but note that the mechanism of sperm competition is not critical in the model in box 1 (though it can be in relation to §3a; see earlier); rather, it is the fact that n males share the probability of fertilization per mating.

4. Consistency: the matings balance and its implications

Darwin's [1] view was that males show indiscriminate eagerness to mate and females show 'coyness' and general reluctance; Bateman [2] attempted to place this notion within a logical framework. The 'higamus hogamus' doggerel (earlier) indicates that this view, applied to humans, is a part of popular Western culture. Its proposition is clearly impossible, because with an adult sex ratio of unity the expected number of matings per male must equal that per female [44,64,71], and many models are constructed on a 'consistent' basis, taking this balance into account, and several are not [72]. Rather, the doggerel represents a statement

Box 1. The effect of polyandry on the difference in male and female Bateman gradients.

Table 2 shows the reproductive success of a mutant male or female that achieves on average $(n + 1)$ matings (column A) compared with that of wild-type individuals in a population where males and females typically have n matings per clutch (column B). Thus, the benefit of the extra mating (column C = columns A − B) is a measure of the Bateman gradient. We take the value of a clutch produced under monogamy ($n = 1$) as one unit of reproductive success. For each additional mating, the expected clutch value (for both sexes) is raised by a constant increment, a, so that when a female receives n ejaculates, the clutch value is $(1 + (n − 1)a)$; when she receives $(n + 1)$ ejaculates, it is $(1 + na)$.

Male fitness is more complex, and depends on how the mutant male gains the extra mating. Suppose that females control matings at n per female, and the mutant male gains his extra mating opportunistically from the total available ejaculates (one per mating male). Thus, each clutch has a value of $(1 + (n − 1)a)$. Provided that an ejaculate can at least potentially fertilize if it occurs in the correct order (e.g. first or last, or whatever), the mechanism of sperm competition is not important and the expected benefits are allocated among the n competing ejaculates giving $(1 + (n − 1)a)/n$; to obtain male fitness we therefore multiply this by the number of matings: in a large population, a rare mutant male gets $(n + 1)$ and a wild-type male gets n matings. The benefit of the extra mating (the male Bateman gradient) is given in column C, case 2, table 2. If we subtract the female gradient (case 1, C, table 2) from the male gradient (case 2, C, table 2) we obtain the difference between the gradients, i.e. $(1 − a)/n$. Thus the female gradient can exceed the male gradient only if $a > 1$, i.e. if each extra mating adds more to clutch value than its total value under monogamy. This seems generally unlikely, even under the most extreme benefits of polyandry for females, and although the difference in gradients is reduced by polyandry, the male gradient is usually likely to exceed that of the female.

If the mutant male gains his extra mating by coercing a female into making an extra mating, he then has n matings with the same fitness gains as a wild-type male, and one mating in which he competes with $(n + 1)$ other males (see A, case 3, table 2) which leads to a different Bateman gradient (C, case 3, table 2). If we again subtract the female gradient (case 1, C, table 2) from the male gradient (case 3, C, table 2), we obtain a difference between the gradients of $(1 − a)/(n + 1)$, which differs in the increased competition $(n + 1)$ in the coerced mating. This dilutes the difference between gradients even further.

Polyandry thus reduces the difference in Bateman gradients, but does not alter which gradient (male or female) is greater (this depends on the relative magnitude of a relative to 1.0). Note that if there is no common benefit conferred on the clutch by extra matings (i.e. $a \rightarrow 0$), the male gradient becomes $1/n$ (case 2) or the lower value $1/(n + 1)$ (case 3), and the female gradient 0 (case 1, C, table 2).

Table 2. Reproductive success of rare mutants that achieve one extra mating (A) compared with wild-type (population) individuals (B), and the Bateman gradients for each sex (C = A − B).

case	A. mutant fitness	B. wild-type fitness	C. Bateman gradient (A − B)
1. female	$(1 + na)$	$(1 + (n − 1)a)$	a
2. male – female control of matings	$(n + 1)(1 + (n − 1)a)/n$	$n(1 + (n − 1)a)/n$	$(1 + (n − 1)a)/n$
3. male – male coerces female into extra mating	$(n(1 + (n − 1)a)/n) +$ $(1 + na)/(n + 1)$	$n(1 + (n − 1)a)/n$	$(1 + na)/(n + 1)$

about behaviour, and refers to the fact that despite this required mathematical equivalence in total matings for males and females, the behaviour of the two sexes (in terms of eagerness, reluctance) at given matings may be very different.

Fisher [73] used self-consistent logic to deduce why the primary sex ratio is unity (because each offspring has a mother and a father, at equilibrium the average fitness of a male must equal that of a female). Expressed in terms of matings, where n_F is the average number of matings per female, and n_M the average matings per male, then where F and M are the numbers of adult females and males in the population,

$$n_F F = n_M M, \tag{4.1}$$

so that if the adult sex ratio is unity ($F = M$), then $n_F = n_M$.

Darwin [1, p. 215] hinted at consistency in the overall expenditures of the two sexes:

The female has to expend much organic matter in the formation of her ova, whereas the male expends much force in fierce contests with his rivals, in wandering about in search of the female. . . . and this expenditure is generally concentrated within a short period. . . . On the whole the expenditure of matter and force by the two sexes is probably nearly equal, though effected in very different ways and at different rates.

Darwin's argument could be expressed in terms of expenditures from a fixed energy budget that is equivalent for the two sexes, but is more simply developed using the logic of 'time in' (i.e. t_I, the average time an individual has available in the mating pool for finding or acquiring matings) and 'time out' (i.e. t_O, the average time an individual is unavailable for mating) [47,74–76]. Using subscripts M, F, to denote male and female, for each female, we assume (simplistically) that when each female mates n times per clutch

$$T = nt_{IF} + t_{OF}. \tag{4.2}$$

This assumes (i) that a female's time out per clutch, t_{OF}, is constant, and (ii) that if it takes a female a time in of t_{IF} to obtain one mating, it will take her time nt_{IF} to obtain n matings. Both assumptions serve as approximations to allow mathematical simplicity (our model is intended only for heuristic purposes): in (i) the proportion of t_{OF} spent actually mating is assumed to be insignificant, which is not true for all species, and in (ii) a more complete formulation would allow t_{IF} to decrease as t_{IM} increases [47].

In contrast, we assume that the male must pay a fixed 'time out' cost (e.g. gamete replenishment time), t_{OM}, each time he mates. Thus, with an adult sex ratio of M/F males per female, each male expects n matings (with an expectation of $1/n$ of a clutch at each one) and hence spends 'time out' of nt_{OM} during a total time of $(M/F)T$. His remaining time t_{IM} is 'time in', so that

$$\left(\frac{M}{F}\right)T = nt_{OM} + t_{IM}. \qquad (4.3)$$

In this population, each male spends time in t_{IM} and each female a time in of nt_{IF} for the production of one clutch. The OSR, or ratio of sexually available males to females, is, therefore, t_{IM}/nt_{IF}. Taking OSR as a measure of the opportunity/strength of sexual selection (which is controversial; see §2), we can see by combining equations (4.2) and (4.3) that the OSR > 1 (i.e. $t_{IM} > nt_{IF}$) when

$$T\left(\frac{M}{F} - 1\right) > nt_{OM} - t_{OF}, \qquad (4.4)$$

which is obviously most likely when the adult sex ratio, $M/F > 1$. Note that the ratio of male PRR, $1/nt_{OM}$, to female PRR, $1/t_{OF}$, is t_{OF}/nt_{OM}. If the adult sex ratio is unity, we require that

$$\frac{t_{OF}}{nt_{OM}} > 1, \qquad (4.5)$$

i.e. that male PRR exceeds female PRR, and if females mate only once per cycle, the condition becomes

$$t_{OF} > t_{OM}, \qquad (4.6)$$

[75], i.e. equivalent to Clutton-Brock & Vincent's [58] claim for PRR. However, the more matings per female cycle, the less likely is equation (4.5) to be satisfied—the reduction by $1/n$ here is equivalent to the reduction in the male Bateman gradient. This simple model demonstrates once again that polyandry reduces the likelihood of sexual selection being more intense on males. However, for species with no male PI, time out for sperm replenishment is likely to be a rather low fraction of the total male time budget, so that equation (4.5) is likely to be robust even when n is relatively high [76].

Is this affected by the mechanism of sperm competition (e.g. sperm mixing, displacement)? Because the expected gain to a male is always $1/n$ of a clutch, at first sight it would appear that these conclusions are again affected only by the number of different male ejaculates per female cycle (the degree of polyandry), and not by the sperm competition mechanism [76]. But, ejaculate allocations are expected to change with the degree of multiple mating n, and there is much evidence that they do so [68,77]. This changes male time out, which affects the conclusions [76], because t_{OM} becomes a function of n and so equation (4.5) should be written as $t_{OF}/n > t_{OM}(n)$. However, this tends to buffer the effect of higher levels of polyandry, because if $n > 2$, sperm allocation, and hence $t_{OM}(n)$, reduces with n [68].

5. Mating decisions, sexual conflict and its resolution

Although at an adult sex ratio of unity, both the average number of matings and average fitness for each male and female must be equal, this does not imply equal benefits of mating to each sex (table 1). A central question is: do females mate multiply because they gain genetic or resource benefits from multiple mating, or simply to reduce costs of rejecting persistent males? Each decision over mating by a given individual depends on its own circumstances, and that of its potential partner [74,78–81]. If 'why polyandry' must be answered generally for a given species, it can be addressed only by analysis of the probability distribution of all possible encounters between pairs of males and females in a population in relation to the male and female states characterizing each pairing. Some encounters will be marked by no conflict (when it pays both male and female to mate, or it pays neither to mate), whereas others will involve sexual conflict in which it pays one sex to mate, but not the other [74,78,79], and in many cases there is the further complication, if mating is favourable, of how much to invest in a given mating. The sum of all these probabilities and outcomes (including those involving sexual conflict) will generate the mean degree of polyandry in a population. There are various ways in which the DBP assertion of being 'more choosy' or being 'more reluctant to mate' can be interpreted. Typically, this has been interpreted in terms of female fitness being highly influenced by male mate quality, favouring mate choice, whereas male fitness is maximized by little or no choice, owing to the sexual asymmetries associated with PI for the two sexes [74,78]. A second way that DBP can be satisfied occurs when sexually conflicted encounters more commonly involve cases when the male benefits directly from the mating but the female does not, than when the reverse applies.

A 'mating decision' [78,79] can be defined as the strategic decision whether to mate or not to mate on encountering an individual of the opposite sex. It defines an individual's best option, independent of the partner's actions. The value of a mating, V, is expressed as a fitness opportunity cost difference between mating and not mating [73,77]. If $V > 0$, the decision is 'mate', and if $V < 0$, it is 'not mate'. (Whether mating actually occurs also on the partner's decision and, if there is conflict between decisions, how this is resolved.) Thus defined, mating decisions specify the parameter space for sexual conflict over mating (the 'zone of conflict'). Note that the opportunity costs, respectively, V_{Mij}, V_{Fij}, for male i meeting female j, are related to the Bateman gradients (reproductive success divided by a unit increase in mate number), for a specified pairing, i,j.

Sexual conflict occurs when either

$$V_{Mij} > 0 \quad \text{and} \quad V_{Fij} < 0; \qquad (5.1)$$
i.e. male benefits but female loses by mating;

$$V_{Mij} < 0 \quad \text{and} \quad V_{Fij} > 0; \qquad (5.2)$$
i.e. female benefits but male loses by mating.

When V_{ij} is positive for each sex, mating is favoured, and when negative for both, it is not. Which pair of conditions applies depends on the set of circumstances operating on

i,j. The zone of conflict ('battleground', *sensu* Godfray [82]) and zones of concordance can be mapped out in parameter space for given situations [74,78]. Parker [74] argued that because of the primordial sex difference, when sexual conflict occurs, it is likely to be of type equation (5.1), and that in most areas of parameter space, males are under stronger selection to mate than females are to resist mating.

Resolution of the conflict is a more complex problem involving either continuous dynamics or stable equilibria (see [74,79,81]), and depends on (i) the value of winning the conflict, measured as the positive deviation of V_{ij} from zero for each partner, and (ii) a measure that has been termed 'power', which relates to the costs of winning [74,79].

There can be many reasons for sexual conflict over mating decisions, and several were identified in the initial analysis [74]. Inbreeding conflict concerns matings between relatives, and sexual selection in relation to inclusive fitness poses special problems [19]. Where the fitness of an outbred offspring is unity and that of an inbred offspring is $(1 - \delta)$, if male PI is insignificant, for brother–sister pairings the brother should mate if $\delta < 2/3$, but his sister should not mate unless $\delta < 1/3$, leading to conflict when $2/3 > \delta > 1/3$ [74]. Recent, more advanced models show that the conflict zone can be modified by the mechanism of choice and the degree of relative PI [79,83]. Meetings between different eco-types or sibling species A and B will yield sexual asymmetries in V_{ij}, and will depend on which sex is A or B. With zero male PI, males are expected to be selected to mate across ecotypes, but females not, suggesting that female behaviour may be selected in a direction favouring speciation, whereas male behaviour may selected towards preventing it by increasing gene flow [74,84].

Sexual conflict can also occur in mating decisions where individuals of a given sex vary continuously (for a large population) in their mate quality, Q, where Q is a measure of the fitness value of an individual of one sex from the per-spective of a member of the opposite sex. The earliest models of mate choice focused on cases where only one sex is choosy [74,85]. Parker [74,78] argued that the variance in mate qual-ity Q of each sex is a critical determinant of mate choice. The optimal threshold for mate quality (Q_{opt}), below which lower quality mates ($Q < Q_{opt}$) should be rejected, depends on the time (or energy) to find an alternative mate and the variance in Q. For instance, if only males in the top 25 per cent are acceptable, with an adult sex ratio of unity and one mating per cycle ($n = 1$), a female must spend on average the equiv-alent of four times in ($4t_{IF}$) to find an acceptable male, i.e. she must on average sample four males to achieve the extra benefit conferred by being choosy compared with mating randomly. For the same degree of choice, the male would sample four females, i.e. spend $4t_{IM}$. With zero male PI, it is clear that choosiness will be much more costly for the male than the female (because $t_{IM} \gg t_{IF}$), so unless the benefits of choice are much greater for the male, choosiness is *a priori* much more probably to be favoured in females. From the disparity in times in (i.e. $t_{IM} \gg t_{IF}$), it is most prob-ably that equation (5.1) will apply for mate choice, i.e. the male will be selected to attempt to mate and the female *j* to resist, fitting the DBP.

However, the greater the variance in mate quality (Q), (i) the more likely a sex is to be choosy, and (ii) if mate choice is favoured, the choosier it is optimal to be (i.e. the lower the value of Q_{opt}). Although the odds are in favour of DBP, with female being choosy and males indiscriminate, this scenario can reverse if the variance in Q is sufficiently high in females and low in males. When both sexes are choosy, assortative pairing for mate quality is often likely [78]. There has been extensive development of mutual mate choice models (see review [79]). The point is that if variance in female mate quality is very high and in males very low, this can reverse the effects of the high female–low male PI disparity that underlies DBP. But whether, and if so, how commonly, this ever applies in nature in another matter.

One way that females can overcome the cost of repeated mate search is to mate indiscriminately, and select ejaculates or sperm by cryptic female choice [32,86,87].

6. Conflict resolution, coercion and acquiescence

Resolution of conflict over mating is a complex topic and beyond the scope of the present review. Solutions range between continuous evolutionary chases to ESS armament levels (see review [79]), with coercion being apparent in many taxa [88].

Since the initial analysis [74], there has been a tendency to summarize mating conflict in terms of a difference in optimal mating rate between the sexes, with selection on males towards higher mating rate optima than females. This approach gener-alizes what is in fact a specific problem relating to mating decisions and possible conflict resolution at each specific pair-ing *i,j*. Although it can be in female interests to mate multiply with an optimal number of males, it can often be disadvanta-geous for a given female to mate with a given male. The reverse is also possible, but because of the primordial asym-metry arising from anisogamy, the zone of conditions across which it pays given females to mate with given males is typi-cally smaller than the zone across which it pays given males to mate with given females, unless special conditions apply (e.g. high variance in female mate quality [78]). The concept of an optimal mating rate difference between males and females does not adequately cover mating conflict; this is focus of a review by Brennan & Prum [89].

Sometimes it can pay females to acquiesce to mating simply to gain respite from harassment. For example, gravid female dung flies *Scatophaga* (=*Scathophaga*) *stercoraria* mate each time they arrive at the oviposition site (a dropping) despite usually containing enough stored sperm for fertiliza-tion of several future clutches. After mating, the male shows paternity guarding, dispelling attacking males, whereas the female oviposits. Calculations taking account of the encoun-ter rate of ovipositing females with males searching on the dropping, and the expected mean time it would take to reject such males, showed that allowing a male to mate in order to gain his guarding during oviposition results in an average time gain to the female of around 50 min per ovipo-sition cycle [90]. Many similar cases where females can actually gain by polyandry as a consequence of avoidance of harassment have been found since this early example.

7. An example: the history of avian polyandry research

Most studies of polyandry have been conducted on birds and insects. Whether females copulated with more than one male

was not considered of much biological significance until the advent of individual selection thinking, when the evolutionary significance of such 'polyandry' became apparent [2,32,91].

Birds have long been popular for study because of their observability, and since long before Darwin's [1] day it was generally assumed that most species were socially monogamous, with a small number of species being polygamous. In a survey by Shufeldt [92], no species were definitely known to have a polyandrous mating system (as distinct from being polyandrous and copulating with several males (above), which was also not considered). A survey by Lack [93] reported that over 90 per cent of all bird species had a monogamous mating system. This was before it was considered likely that females of socially monogamous species could be promiscuous or polyandrous. One consequence of the behavioural ecology revolution was the recognition that promiscuity, especially by males, might be widespread, as indeed it proved to be [94,95]. As with the insects, much of the original thinking in terms of adaptive explanation was male-orientated.

An important turning point was when Smith [96] reported that female black-capped chickadees, *Parus atricapillus*, seemed to actively seek extra-pair copulations, and from males of higher social rank than the female's partner. These behavioural observations, accumulated opportunistically over several years of fieldwork on individually colour-ringed birds, provided the first evidence that, contrary to the view then prevalent, females might benefit from engaging in extra-pair copulations. Subsequent studies confirmed that extra-pair paternity occurred in chickadees, and other researchers were quick to seek—and find—evidence for female-initiated extra-pair behaviour in other species [97], and to seek adaptive explanations for it. In what was probably a case of a bandwagon effect [98,99] it gradually became accepted that many or most extra-pair copulations in birds were initiated by females until Westneat & Stewart [100] re-assessed the situation and concluded that the incidence of solicitation of extra-pair copulation by females was exaggerated.

Nonetheless, Smith's study raised the possibility that if females actively seek extra-pair copulations they might also possess mechanisms to ensure that the sperm from extra-pair males fertilized their ova. This in turn led to a more serious consideration of cryptic female choice: the idea, first proposed by Thornhill [86] and later extensively evaluated by Eberhard [32], that polyandrous females might possesses mechanisms to control which sperm fertilized their ova. The rise in interest in cryptic female choice coincided not only with an increasing emphasis on female processes in behavioural ecology, but also spearheaded a move to better understand the anatomical and physiological mechanisms of post-copulatory sexual selection, which in turn became part of behavioural ecology's broader horizon [101].

While it seems to be the case that most extra-pair copulations in birds are not initiated by females, in some instances, as in Smith's [96] chickadees, they clearly are, and it is these species (or instances) where attention would be best focused to ascertain the possible benefits. So far, most studies directed towards identifying potential indirect female benefits have been conducted on species that are convenient for other reasons rather than because behavioural observations provide a sensible justification. However, we need to add a caveat to this: female sexual behaviour is often much more subtle than male behaviour, and behaviours associated with polyandry may be easily overlooked. Several studies of a variety of taxa including mammals, birds, invertebrates, have reported indirect female benefits of polyandry. However, what is striking about these studies, and especially those on birds, is that there seems to be no consensus of the indirect benefit [98]. Some studies report a higher rate of growth among extra-pair offspring in mixed paternity broods; others might report no difference in growth, but a better immune response in extra-par offspring, and so on. As the prize for discovering what 'the' indirect benefit of extra-pair copulation is remains increasingly elusive, studies seeking it have become more and more elaborate and impressive; e.g. in a study of extra-pair paternity in the coal tit, *Parus ater*, Lubjuhn [102] conducted paternity analyses on 483 broods comprising 3559 offspring. Reid & Sardell [103] used multi-generational data from a detailed long-term study of song sparrows, *Melospiza melodia*, to check for indirect female benefits, but instead found indirect costs.

In the light of this lack of any convincing evidence that females gain indirect benefits from extra-pair copulations, it remains a possibility for certain bird species at least that both the costs and benefits of extra-pair copulations for females are relatively small. If we consider the distribution of extra-pair offspring (the proportion of all offspring in a population that are extra pair) across species [104], we find: (i) within-species, levels of extra-pair paternity are repeatable; (ii) some species are monogamous (zero extra-pair paternity); (iii) some species show low to medium levels of extra-pair paternity, although not all females produce extra-pair offspring, and (iv) a small number of species show high levels of extra-pair paternity (greater than 65%).

Given the amount of effort that has been invested in such studies and the lack of evidence that females gain indirect benefits, it may be time to consider alternative explanations. Among the first to suggest that low levels of extra-pair paternity have no selective advantage for female birds was Reyer *et al.* [105] for Alpine water pipits, *Anthus spinoletta*. During the period when copulations take place, both sexes can be highly motivated to copulate: it may simply be less costly for females to acquiesce and engage in an extra-pair copulation than to spend time and energy rebutting a persistent male (as described in §6 for certain insects). This, of course, implies that it matters relatively little to the female who fathers her offspring, which appears to be consistent with the results of numerous studies. This in turn not only raises the question, but also generates some specific hypotheses, for why in certain species it does appear to matter and females go to extraordinary lengths to avoid extra-pair copulations and extra-pair fertilizations. In contrast, in certain mammals such as ground squirrels, females that copulate with multiple males produce more offspring [106], an intriguing observation whose mechanism remains to be explained.

In a small proportion of birds, forced extra-pair copulations occur. It was once assumed that because the males of most bird species do not possess a penis, such forced copulations would be ineffectual (raising the question of why they do it at all). As subsequent studies showed [107], this is not true. It is precisely in those species where forced extra-pair copulations occur where we might expect to see cryptic female choice. The females of most bird species choose which male will father their offspring through pre-copulatory mechanisms, but where males are able to override such mechanisms, we might expect to find cryptic female choice.

In feral fowl, females preferentially copulate with the socially dominant male. However, because males are much larger than females, subordinate males attempt to forcibly inseminate females, despite a series of avoidance tactics by females. Even if subordinate males successfully inseminate females, the females are able to physically eject their semen [107].

Similarly, in certain ducks, forced extra-pair copulations are common [108,109], with the additional twist that males in these birds have a phallus. In some species the phallus is enormous and as long as the male's body, and across species relative phallus length appears to covary with the incidence of forced extra-pair copulation [110]. Forced extra-pair copulation is extremely costly for female ducks which go to extraordinary lengths to avoid it, and because many copulations occur on water, some females are drowned as a result of multi-male extra-pair attempts [108]. In response to this, females have evolved elaborate anatomical adaptations that appear to minimize the likelihood of fertilization from a forced extra-pair copulation. In virtually all other birds, the vagina is a simple tube-like structure. But in certain waterfowl the vagina has up to three side branches and a spiral structure at the junction of the vagina and uterus in the region near the location of the sperm storage tubules. The degree of elaboration of vagina covaries, across duck species, with phallus length [111]. Moreover, the phallus is a spiral-shaped structure, but spirals counter-clockwise whereas the vagina spirals clockwise. Brennan *et al.* [111] speculate that during pair copulations the female relaxes the vaginal muscles to permit effective penetration, but during forced extra-pair copulations contraction of the vaginal spiral diverts the phallus into one or other of the vaginal side branches [111]. Many questions relating to this phenomenon still require answers, including the question of why avoiding forced extra-pair copulations is so important to female ducks.

The anatomical adaptations that female ducks employ to minimize the effectiveness of forced extra-pair copulations contrast with the situation in feral fowl, where in the absence of overt anatomical adaptations females respond behaviourally by simply ejecting ejaculates of unwanted males [107]. These two examples illustrate rather different mechanisms within a single taxon and undoubtedly others will be discovered. Not only does the incidence of polyandry, voluntary or coerced, differ between taxa, the mechanisms that evolve in response to it also vary. By comparison with insects, birds are relatively uniform: the diversity of reproductive traits within insects is extraordinary [32,112].

8. Polyandry and subjectivity

If ever a subject deserved the attention of the philosophers of science, it must be that of polyandry. Undoubtedly, some biases in interpretations of sex differences in propensity to mate multiplicity are likely to have occurred due to sexual stereotypy, and to the fact that much of the early work on sexual selection was done by men, including the founders,

Darwin and Bateman. Since then, Trivers's [29] classic paper on PI and sexual selection, and the early works on sperm competition [91] and sexual conflict [74], probably continued this bias [113]. However, it is notable that the pioneers [86,87] and the chief protagonist of cryptic female choice [32] were also men. The claims that terminology and approaches used in sexual selection are male-biased leading to misconceptions have been largely (but certainly not exclusively) made by female researchers [114–116], who have also made pioneering advances [114,117]. Recently, notable bias though sex stereotypy has been claimed for sexual conflict [25,27], a claim incisively attacked by Perry & Rowe [26]. Objectivity (by both male and female researchers) appears to be more difficult to attain in sexual selection than in, say, particle physics.

Our own view is that while these contributions have been important in leading to a better understanding of the adaptive nature of polyandry in particular and female sexual strategy in general, they add to our insight but have certainly not invalidated DBP as a general first expectation for species with zero or low male parental care. For instance, we endorse the so-called 'gender-neutral' model of Gowaty & Hubbell [29], because it seeks to predict behaviour of each mating partner (i,j) on a basis of the specific set of constraints on the two partners. To this extent, it is similar to the approach of Parker [74,78] that also attempted to deduce optimal behaviour at the level of specific paired i,j interactions (see §5). However, we disagree with the claim that the 'gender-neutral' approach implies that sex roles have no basis in anisogamy, for all the reasons so cogently argued by Schärer *et al.* [8]. Sex roles are normally related directly to relative gametic expenditures, though parental care *per se* (which is not a ubiquitous phenomenon) can indeed be finely balanced to shift to one sex or the other if the ecological circumstances are favourable [118]. Even then, prior biological conditions relating to anisogamy and mode of fertilization are likely to have had much impact on when these conditions occur, as Smith [118] discussed. Given the vast differences between the mating partners owing to the primordial sex differences, we doubt if the 'gender-neutral' model will negate DBP. As with a great deal of progress in science, the extensive debate and the explosion of research of the past decades have greatly amplified and refined our understanding of sexual selection, mating strategies, and sexual conflict, rather than replaced them with new paradigms.

Note added in proof

While the present paper was in press, Kokko *et al.* [119] have independently published a detailed analysis of the effects of the relationships between OSR and male time out on sexual selection intensity which investigates more fully the sort of effect (and others) illustrated in §2, paragraph 7.

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