

# On the resolution of the lek paradox

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**Directional female mate choice is expected to deplete additive genetic variation in male traits. This should preclude such trait-based choice from resulting in genetic benefits to offspring, and yet genetic benefits are the explanation for the choice. This evolutionary conundrum is known as the lek paradox. Newly proposed resolutions to this paradox aim to unravel mechanisms that contribute to the persistence of genetic variance in traits under directional female mate choice.**

## Mate choice for additive genetic benefits and the paradox of the lek

Over 100 years of research have shown that sexual selection is a powerful agent of evolution. Nevertheless, the importance of additive genetic benefits (see Glossary) in driving mate-choice evolution remains unresolved [1,2]. Understanding their role is challenging because directional mate choice should erode the additive genetic variance that is a prerequisite for such benefits to occur [3]. This challenge is also known as the ‘lek paradox’: why are females continuing to choose based on additive genetic benefits for the offspring, given that directional female choice depletes additive genetic variation in male traits, thus precluding female choice from resulting in additive genetic benefits for the offspring (Box 1)? The tantalizing nature of the lek paradox has been a significant stimulus behind much evolutionary research [3–6], and here we discuss four recent publications proposing new resolutions of the paradox [7–10].

## Preference for unrelated mates

Reid [10] and Hoffman *et al.* [7] have simultaneously generated similar hypotheses for the role of female preference for unrelated mates in providing genetic benefits of mate choice. Reid [10] observed that, in a small island population of song sparrows (*Melospiza melodia*), females prefer males with larger song repertoire sizes, and such males have lower coefficients of inbreeding ( $f$ ). Crucially, there is a positive correlation between the  $f$  of parents and their offspring [11], and a negative correlation between the repertoire size of the male and his mean kinship to the female population [10]. Hence, by making an assumption about avoidance of close inbreeding (evidence for which is weak [11]), Reid [10] concludes that directional female preference for repertoire size yields genetic benefits in terms of producing outbred offspring. Interestingly,

although Reid argues that the genetic benefits are non-additive, in males with a large repertoire size, the fitness of their offspring is above the population average, which by definition means that such males have a positive breeding value for fitness. This implies that the benefits are actually additive, rather than nonadditive.

Reid [10] is clear about the restrictions to the generality of the above mechanism for benefits of female choice, and summarizes five requirements for it: (i) there must be variation in  $f$  within the population; (ii) the chosen trait must show inbreeding depression; (iii) fitness must decline with inbreeding; (iv) population members must vary in their relatedness to potential mates; and (v) there must be a parent–offspring correlation in  $f$ . The greatest hurdle to the generality of this model relates to the population structure; Reid [10] argues that a parent–offspring correlation in  $f$  is not an inevitable feature of a population but is likely only in small, fragmented or structured populations. Although population structure has previously been incorporated into models of sexual selection, in these earlier models it was in the context of environmental heterogeneity and local adaptation. Here, immigration disrupts local adaptation, and females might evolve choosiness for traits indicating local adaptation [12,13]. Interestingly, Reid’s idea predicts that the offspring of immigrants enjoy the highest fitness, whereas the previous models [12,13] assume that local individuals have highest fitness. Whether immigrants or

## Glossary

**Additive genetic benefit:** an increase in offspring breeding value for fitness over what would be expected if mating was random. Benefits can be accrued through increased attractiveness or viability of the offspring. Additive genetic benefits are always expressed in, and must be measured from, offspring fitness.

**Additive genetic variance:** variance of breeding values in a population. This is strictly a property of a population that can not be measured from an individual.

**Breeding value:** the breeding value of an individual is twice the expected deviation of the mean trait value of the progeny of an individual from the mean trait value of a randomly mating population. Breeding value is a property of an individual but the value of the individual depends on the population from which the mates of the individual are drawn.

**Coefficient of inbreeding:** the probability that the two alleles at any given locus in an individual are identical by descent. It expresses the degree of relatedness of the parents of the individual and is equal to the coefficient of coancestry or coefficient of kinship between the two parents.

**Directional female mate choice:** mate choice in which all females target the same extreme trait values (e.g. large song repertoire in birds).

**Genic capture:** the costs of maintaining or producing a male trait will make the traits condition dependent, leading to the evolution of a genetic covariance between condition and trait expression. Through this mechanism, traits are believed to ‘capture’ the genetic variance in condition.

**Indirect genetic effect:** indirect genetic effects occur when genes expressed in one individual have effects on the phenotype and fitness of another individual.

### Box 1. Resolution of the lek paradox hides in its premises

The lek paradox has attracted nearly 200 publications and thousands of citations (ISI web of knowledge). Perhaps some perspective is required in our quest to resolve the lek paradox. It is already a decade since Ritchie [15] (see also Reynolds and Gross [16]) pointed out that it is not clear whether the paradox commonly exists, let alone what its resolution might be. Indeed, because the lek paradox is so frequently used as a context for research, it is vital to be clear about what the paradox is, whether it exists and how it can be resolved.

Borgia [17] introduced the 'lek paradox' concept to describe mating systems in which there seems to be no material or other direct benefits of female mate choice. He further stated that the lek paradox consists of an apparent contradiction between theoretical predictions about the depletion of genetic variation in male traits under directional female choice and the existence of genetic benefits of the choice. The paradox is: why are females continuing to choose males based on additive genetic benefits for the offspring, given that directional female choice depletes additive genetic variation in male traits, thus precluding female choice from resulting in additive genetic benefits?

Typical of all paradoxes is that the premises on which they are based are unfounded, in which case the paradox does not really exist, or, alternatively, that one or both of the predictions which lead to the apparent contradiction are not true, in which case the paradox is resolved. Embedded within the lek paradox are three premises: (i) female choice occurs; (ii) there is a cost of female choice; and (iii) there are no direct benefits from the choice, whereas the predictions 'females gain genetic benefits from their choice' and 'female choice depletes genetic variance, precluding the genetic benefits' constitute the apparent contradiction. Any attempt to understand and resolve the lek paradox should first consider the accuracy of its premises.

The existence of female choice seems to be generally accepted, although it is not necessarily clear what constitutes conclusive evidence of it [2]. The cost of choice is vital to the lek paradox because female choice can evolve easily if it is cost free [18]. Note that the cost of female choice must be in terms of reducing female fitness [2]. Most current treatments assume that costly female choice occurs but this has not yet been shown conclusively. The third premise – that there are no direct benefits from female choice – seems simple but might prove impossible to verify empirically. This is because the scientific method can only falsify null hypotheses, not prove them to be correct.

Only if all premises are supported (and, in the case of the lek paradox, they are only partly so), is it relevant to ask how the paradox is resolved, by considering which of the predictions are erroneous. When two predictions contradict each other, proving one of them right means that the other one must be false. If the prediction, 'females gain genetic benefits from their choice', is correct, then the other prediction 'female choice depletes genetic variance, precluding the genetic benefits' must be false, and the paradox is resolved. Interestingly, the resolution is not symmetrical regarding the predictions: if the prediction 'female choice depletes genetic variance, precluding the genetic benefits' is correct, thereby rendering the prediction 'females gain genetic benefits from their choice' false, then there are no genetic benefits from female choice, and the lek paradox will always persist. Consequently, the only resolution of the lek paradox is that the directional selection imposed by female choice is not enough to deplete the genetic variance in fitness. Unravelling the various mechanisms that contribute to the persistence of genetic variance remains an exciting objective, to which the papers discussed here [7–10] offer a significant contribution.

locals are most fit depends on the degree of environmental heterogeneity, on population sizes and on migration rates, which together determine the degree of local adaptation and inbreeding depression.

Although Reid [10] was cautious not to interpret her results directly in the context of the lek paradox, the

implications for it are clear: inbred populations with an occasional migrant from a genetically differentiated population will not go to fixation at fitness-related loci, and, hence, migration combined with inbreeding depression might provide a resolution to the lek paradox.

The idea of Hoffman *et al.* [7] is similar to Reid's, in that they propose that female Antarctic fur seals (*Arctocephalus gazella*) prefer unrelated males of high heterozygosity. The study by Hoffman *et al.* [7], and references therein, report a correlation between the 'internal relatedness' (a measure related to  $f$  and based on heterozygosity data at nine loci) of sires and their offspring. Here, the correlation arises without a mention of any peculiarities of population genetic structure, although these might occur [7]. Nevertheless, the correlation is weak, and the benefits to females of choosing relatively outbred males are weakened further by the small effect sizes of internal relatedness on male fitness, and the absence of an association with female fitness. Hoffman *et al.* argue that the low heritability of heterozygosity means that heterozygosity will not lose variability under directional selection, thus resolving the lek paradox. However, this is a restatement of the paradox, rather than its resolution: females prefer a trait with low heritability, precluding choice from providing sufficient genetic benefits, yet genetic benefits are the explanation for the choice. The second resolution of Hoffman *et al.* [7] to the lek paradox is inbreeding avoidance causing females to favour different males. However, if females prefer different males, no directional female choice exists, and the concept of the lek paradox does not apply.

Regardless of any deficiencies in the data that the armchair pedant might seize upon, the arguments of both Reid and Hoffman *et al.* deserve further theoretical and empirical attention. Their ideas might prove to be important in terms of how fitness variation is maintained, perhaps even when the restrictive conditions of the lek paradox are met (Box 1).

### Evolving mutation rates

In stark contrast to the current paradigm, according to which female choice depletes genetic variance in male traits, Petrie and Roberts [8] propose that female choice increases genetic variability by favouring modifiers that increase mutation rates in loci determining viability and sexual trait expression. In their simulation model, the increase in mutation rates evolves because female choice for the 'best-of- $n$ ' males strongly favours beneficial mutations, and linked modifiers of mutation rate hitch-hike with the beneficial mutations to high frequency. The idea that strong directional female choice can select for modifiers increasing the genetic variance in the trait is not new [4], although selection on modifiers of mutation rate is. However, for the model of Petrie and Roberts to work, restrictive assumptions have to be met – for example, tight linkage between the modifier and the loci determining fitness [14].

Costly female choice is a fundamental premise of the lek paradox (Box 1), and this should be considered by any theoretical or empirical treatment. Although they touch upon the issue, Petrie and Roberts' model [8] does not convincingly incorporate the cost of female choice: the model seems to assume that choosing the best-of-two or the best-of-20 carries the same cost. Including a cost of

choice in sexual selection models often alters the dynamics and outcomes of the models. Also, in this model, female choice was not able to evolve but was set to be a constant 'best-of-n' strategy. Nevertheless, the number of beneficial mutations increased with increasing strength of female choice, suggesting that this mechanism creates positive selection for female choice. This is because stronger female choice seems to return greater benefits. To determine whether the positive feedback between female choice and the benefits of choice can provide a self-sustaining resolution to the lek paradox, a dynamic model enabling the evolution of female choice and incorporating a cost of choice will be necessary.

### Indirect genetic effects

Miller and Moore [9] develop the genic-capture idea of Rowe and Houle [5]. The principal thesis of Miller and Moore [9] is that, in addition to the direct genetic effects influencing offspring condition, there are also indirect genetic effects. They provide a simple but convincing example: mothers influence the environment of their offspring, and, hence, offspring phenotypic condition and condition-dependent display traits, and the variation among mothers in their influence has a genetic basis. The authors suggest that the aim of female choice for mates with elaborate traits might be to obtain good genes for daughters in terms of effective parenting characteristics. The contribution of maternal performance to offspring condition and, hence, condition-dependent display traits is likely to be large in many species and has, until now, been mostly overlooked. The persistence of additive genetic variances in maternal characteristics under these circumstances is yet to be explored empirically. Nevertheless, the female choice component of this model requires that the non-genetic environmental effects on maternal parenting characteristics are relatively low because otherwise they will swamp the influence of the good maternal parenting genes of the mother of the chosen male. This, and the dilution of the parenting genes (the offspring of the choosing female inherit only a quarter of the parenting genes), might prove to be restrictive requirements.

### Conclusion

The only resolution of the lek paradox is that the directional selection imposed by female choice is not enough to deplete the genetic variance in fitness (Box 1). This is exactly the focus of the four papers discussed: unravelling

the mechanisms that contribute to the persistence of genetic variance under directional female choice. One of the most promising avenues for future research is to determine the generality of additive genetic benefits from female choice for heterozygous males. The answer to this question will crucially depend on how often, and under what conditions, heterozygosity, or the coefficient of inbreeding, is heritable.

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