



## FORUM

## On female choice, heterozygosity and the lek paradox

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One of the major unresolved issues in the theory of sexual selection is the importance of indirect genetic benefits as a driving force of mate choice (Andersson & Simmons 2006; Charmantier & Sheldon 2006; Qvarnström et al. 2006; Kotiaho 2007; Kotiaho & Puurtinen 2007). Elucidating their role is challenging because the directional selection imposed by mate choice should erode the genetic variance that is the prerequisite for the indirect genetic benefits. This is also known as the ‘lek paradox’: female choice depletes genetic variation, thus leaving little room for choice to result in genetic benefits, and yet the genetic benefits are the explanation for that choice (Kotiaho et al. 2001; Tomkins et al. 2004). In their recent paper, Hoffman et al. (2007) argue that they help to resolve the lek paradox in Antarctic fur seals by showing that active female choice operates to maximize the balance between male high heterozygosity and low relatedness. This finding is proposed to provide a resolution first because heterozygosity has low heritability which means that the variability in heterozygosity will not be eroded by the directional selection imposed by female choice and second because inbreeding avoidance means that different females will favour different males. The purpose of our commentary is to draw attention to two issues that may undermine the theoretical framework in which Hoffman et al. (2007) have framed their study and to propose an alternative explanation for the observed patterns.

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The theoretical framework in which Hoffman et al. (2007) have framed their study hinges on there being active female choice. We suggest that there is no evidence of female choice in Antarctic fur seals and consequently the existence of the lek paradox in this system is doubtful. Hoffman et al. (2007) argue that the observation that some females are impregnated by males that are up to 35 m away from the female’s pupping location on the day of conception constitutes evidence for active female mate choice. They back their argument with a reference to their earlier work by stating that ‘whereas females are reasonably mobile, males rarely move more than a body-length (2 m) during the main part of the breeding season (Hoffman et al. 2006b)’. The cited paper states that the distance between daily sightings of males is on average 1.6 m and that of females on average 3.0 m, the median being less than 2 m for both sexes (Figure 1a, c in Hoffman et al. 2006b). Moreover, in the same Figure 1a, there is evidence that some males are sighted up to 20 m from the position where they were seen on the previous day. Apart from the obvious problem that distances between daily sightings may not accurately estimate the movement of animals, it appears that both sexes are rather static but that occasionally either sex may move up to 20–30 m. Therefore, we feel it is not possible to conclude that it is the females, rather than the males, who are moving and responsible for the negative relationship between distance and internal relatedness of the father.

Even if one were to accept that females were the gender that moved, interpreting the distance moved as a measure of preference is problematic. This is because approximately 75% of females mated within 6 m and only approximately 8% travelled more than 10 m to mate (Hoffman et al. 2007). If moving a greater distance is taken as an indication of females mating with the preferred

male, the data show that the great majority of the females choose to mate with a nonpreferred male. Hoffman et al. (2007) suggest that females that mate with the closest males may not be choosy or have already exercised choice when choosing where to pup. Although Hoffman et al. (2007) tend to favour the latter explanation, we feel this cannot be the true explanation: if most females had already exercised choice for high heterozygosity (thus not needing to travel) we would not expect a relationship between distance and heterozygosity. Alternatively, if the great majority of females that did not travel far were not choosy, the strength of directional selection imposed by female choice required under the lek paradox simply would not exist in the population. We suggest that to determine whether the realized parentage is even compatible with a female preference for heterozygosity and relatedness, in the manner that Hoffman et al. (2007) are suggesting, the authors should have compared the heterozygosity and relatedness of the chosen males to those of the available males that the female did not choose, i.e. the males that are within the radius of the distance the female apparently travelled to mate. According to Figure 2 in Hoffman et al. (2007) these data are available to the authors.

The lek paradox, around which Hoffman et al. (2007) have framed their study, has been proposed to be resolved by the observation that, despite directional female choice, additive genetic variation in the selected traits persists (Pomiankowski & Møller 1995). The currently most supported mechanism that accounts for this observation is the genic capture mechanism (Rowe & Houle 1996), where the genetic variance in sexually selected traits is dependent upon all loci throughout the genome that contribute to the acquisition of resources. Because of the great abundance of these loci, the genesis of new mutations is frequent enough to provide a constant source of variation. Hence the paradox is resolved because heritability in the trait can be maintained and thus female choice can result in indirect genetic benefits. Hoffman et al. (2007) note that this resolution to the lek paradox is somewhat unsatisfactory and that in this resolution the low heritability of the trait is the key to the avoidance of the loss of additive genetic variance. In contrast to Hoffman et al.'s (2007) statement, however, the maintenance of the additive genetic variance and hence persistent heritability is the key and low heritability would actually be the cause of the paradox.

Along the same line of reasoning, Hoffman et al. (2007) suggest that they help to resolve the lek paradox in two ways: first, because, even though directional female choice apparently operates to create offspring with high heterozygosity, the low heritability of heterozygosity means that the variability in heterozygosity will not be lost and, second, because of the inbreeding avoidance, different females often favour different males.

The first argument seems to be a restatement of the paradox rather than its' resolution: females prefer a trait with low heritability, precluding choice from providing genetic benefits, yet genetic benefits are the explanation for the choice. Moreover, Hoffman et al. (2007) suggest that in this system the cost of female choice may be

substantial in terms of increased risk of offspring mortality and note that therefore larger movements should be made only in return for greater genetic benefits. Hoffman et al. (2007) do not directly analyse the magnitude of the genetic benefit but instead report a weak relationship between male internal relatedness and parental relatedness (proxies for male and offspring heterozygosity, respectively). The magnitude of the effect in this relationship is modest at most, male internal relatedness explaining 2.9% of the variance in parental relatedness (Hoffman et al. 2007). It should be noted, however, that parental relatedness is not equivalent to offspring heterozygosity and that offspring heterozygosity is not equivalent to fitness. Indeed, in the study population, parental relatedness explains 23.0% of the variance in offspring heterozygosity (measured as offspring internal relatedness; Hoffman et al. 2006a) and heterozygosity explains 4.7% of the variance in male long-term reproductive success (calculated from  $F_{1,390} = 19.44$  in Hoffman et al. 2004). To determine whether indirect benefits exist, the direct relationship between sire internal relatedness and offspring fitness should be analysed.

If we consider the fitness benefits that a choosy female might be gaining in this system, it appears that her male offspring's reproductive success is likely to be a relatively good measure of the fitness benefit. This is because heterozygosity of a female is not an important determinant of her fitness and offspring heterozygosity is not an important determinant of offspring survival (Hoffman et al. 2006a). Although multiplication of the above variances as explained can give only a rough estimate of the magnitude of the fitness benefit that choosy females might gain, the suggestion is that the benefit is practically nonexistent ( $r^2 = 0.0003$ ). That this benefit accrues to only half of the female's offspring (males) should also be considered. Therefore, provided that there was costly female choice in this system and that the fitness benefit from this choice was nonexistent, Hoffman et al. (2007) would provide just another example of lek paradox rather than help to resolve it.

The second argument, that different females often favour different males, resorts to females basing their choice on inbreeding avoidance or genetic compatibility (Tregenza & Wedell 2000; Colegrave et al. 2002; Neff & Pitcher 2005; Puurtinen et al. 2005). The concept of genetic compatibility, of which inbreeding avoidance can be considered a special case, rests on the idea that females may gain indirect genetic benefits by choosing a mate that has alleles which in combination with her own alleles yield offspring that have better than average fitness. Because it is the interaction between female and male genotypes that determine the genetic value of the offspring, this mechanism does not lead to erosion of genetic variance in preferred traits because there can be no directional selection for any trait. Therefore, in mating systems where this mechanism operates, the first premise of the lek paradox, i.e. that directional selection should erode variance, is not met and thus in these mating systems the whole concept of lek paradox is not pertinent. We agree that showing in a particular mating system that female choice is for compatibility and thus does not cause directional

selection does mean that there is no lek paradox, but at the same time we do not agree that this is the resolution of the lek paradox because it does not remove the fact that there are other mating systems in which female choice does result in directional selection.

We also note that there may be complications in the methods of the Hoffman et al. (2007) study. Recently it was shown that negative relationships between heterozygosity and parental relatedness arise for purely computational reasons (Roberts et al. 2006), questioning the biological significance of the reported (Hoffman et al. 2007) interaction. However, as Roberts et al. (2006) did not investigate the measure of heterozygosity (internal relatedness) used in Hoffman et al.'s (2007) work, whether the negative relationship between heterozygosity and relatedness reported is indeed an artefact or a real biological phenomena remains to be seen. Also the failure of the authors' microsatellite loci to reflect genome-wide effects (Hoffman et al. 2006a) undermines their use in the way that the authors have used them, thus further compromising their conclusions (Balloux et al. 2004).

We conclude that the existence of active female choice in Antarctic fur seals is doubtful and that in mating systems where there is no directional female choice there can be no lek paradox. We feel that a more parsimonious explanation for the relationship between distance and male heterozygosity is that more heterozygous males are able to win matings further from their own territory. Indeed, this is plausible since heterozygosity positively influences male competitive ability (Hoffman et al. 2004). Provided that it is the males and not the females who are moving, the observed pattern would thus easily emerge without the need for active female choice for heterozygosity based on an unknown mechanism.

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