ORIGINAL ARTICLE

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Imperfect female choice and male mating skew on leks of different sizes

Abstract We present a model of error-prone female choice on leks, and investigate the effects of different degrees of error on the distribution of mating success among males present at leks of different sizes. At higher levels of error, the best male is predicted to gain a smaller share of matings, while low-ranking males gain a larger share. Males who are of high rank but not the most desirable on the lek do best at intermediate levels of error, since the top-ranked male does not then claim all the matings, but assessment is still sufficiently accurate for females to discriminate between high-ranking and low-ranking competitors. The effects of error are shown to be more pronounced on larger leks, due to smaller expected differences in mating value between males of adjacent ranks. This interaction between lek size and error suggests that observed negative relationships between lek size and mating skew need not be attributed solely to intrasexual competition, as previously suggested, but could also be a result of imperfect choice.

Key words Mate choice · Sexual selection · Lekking

Introduction

One of the characteristic features of leks is the high variance in mating success among males within each aggregation (Höglund and Alatalo 1995; Wiley 1991). This variance is often attributed to female choice, which leads to more attractive males receiving a disproportionate share of matings (Bradbury and Gibson 1983; Höglund and Alatalo 1995; Wiley 1991). A number of studies, however, have found that the degree of male

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mating skew is greater on smaller leks, where male dominance relationships are more clearly defined (e.g. Alatalo et al. 1992; Höglund et al. 1993; Widemo and Owens 1995). This pattern seems to support the idea that the distribution of matings may be as strongly or more strongly influenced by intrasexual competition than by intersexual choice (Alatalo et al. 1992; Höglund et al. 1993; Widemo and Owens 1995).

In this paper, we consider the alternative possibility that reduced male mating skew on larger leks is a consequence of imperfect female choice, rather than (or in addition to) male-male competition or interference (Höglund and Alatalo 1995). In the last few years, models and discussions of female choice tactics have increasingly begun to recognize the importance of errors and uncertainty in female assessment of males (Getty 1996; Johnstone 1997; Luttbeg 1996; Sullivan 1994), yet there has been little attempt to investigate the consequences of such uncertainty for the distribution of male mating success (though see Bradbury et al. 1985; Mackenzie et al. 1995a). Here, we outline a model of imperfect female choice on leks, and investigate the predicted effects of assessment error on the distribution of expected mating success among males, on leks of different sizes.

The model

Males on a lek vary in mating quality, denoted q. This variation could reflect differences in age, dominance, vigour, parasite resistance and/or any other unspecified traits that yield direct or indirect mating benefits. The only assumption we make is that the traits contributing to quality are universally desirable, i.e. that a higher-quality male is of greater value to all potential partners. The qualities of individual males are independently drawn from the probability distribution $f(q)$; the cumulative probability distribution of qualities will be denoted $F(q)$.

Females visiting a lek assess the quality of each of the males present, and choose to mate with the individual of apparently highest value, i.e. they adopt a 'best-of-n' choice strategy, appropriate when the costs of choice are slight (Janetos 1980; Real 1990; Wittenberger 1983). Each female is assumed to make her choice

independently, so that there is no mate choice copying (Gibson and Höglund 1992; Losey et al. 1986; Pruett-Jones 1992). Different females may choose different males on the same lek, because female assessment of male quality (which could be based on any number of cues, including e.g. territory centrality, ornamentation, size, or the vigour of display) is error prone. That is, the perceived quality of a male, denoted p, is not necessarily equal to his true quality. The probability distribution of p given q will be denoted $g(p|q)$; the corresponding cumulative distribution, which specifies the probability that a male of quality q is perceived to be of quality p or less, will be denoted $G(p|q)$.

We wish to determine, under the above circumstances, the expected distribution of matings among males on a lek of size n. Let $m(n,i)$ denote the expected share of matings obtained by the male that is ranked ith in terms of quality on such a lek. Since females make their choices independently, this is simply equal to the probability that an individual female will perceive the ith-ranking male to be the best present. To specify this probability, we need to define two new functions. The first, which we denote $H(p,q)$, specifies the probability that a randomly chosen male will be of perceived quality less than p and true quality less than q, and is given by

$$H(p,q) = \int_{x<q} f(x)G(p|x)\mathrm{d}x \tag{1a}$$

The second, which we denote $J(p,q)$, specifies the probability that a randomly chosen male will be of perceived quality less than p and true quality *greater* than q, and is given by

$$J(p,q) = \int_{x>q} f(x)G(p|x)\mathrm{d}x \tag{1b}$$

Using these functions $H(p,q)$ and $J(p,q)$, we can specify the probability that a male of true quality q and perceived quality p, on a lek of size n, will prove to be the top-ranking individual in terms of perceived quality and the ith-ranking individual in terms of true quality. This is given by

$$\binom{n-1}{n-i} H(p,q)^{n-i} J(p,q)^{i-1} \tag{2}$$

which is the probability that $n-i$ of the remaining $n-1$ males are of lower perceived quality and lower true quality, while $i-1$ are of lower perceived quality but higher true quality.

Integrating over all possible combinations of true and perceived quality, we obtain the probability that a randomly chosen male on a lek of size n will prove to be the top-ranking individual in terms of perceived quality and the ith-ranking individual in terms of true quality

$$\binom{n-1}{n-i} \int \int f(q)g(p|q)H(p,q)^{n-i} J(p,q)^{i-1} \mathrm{d}p\,\mathrm{d}q \tag{3}$$

Finally, dividing by the probability that a randomly chosen male is the ith-ranking individual in terms of true quality, which is simply equal to $1/n$, we obtain $m(n,i)$, the probability that a male is perceived to be the best mate present on a lek of size n, given that he is ranked ith in terms of quality on that lek

$$m(n,i) = n\binom{n-1}{n-i}$$
$$\times \int \int f(q)g(p|q)H(p,q)^{n-i} J(p,q)^{i-1} \mathrm{d}p\,\mathrm{d}q \tag{4}$$

Results

To evaluate Eq. 4, we need to specify both the distribution of male qualities, $f(q)$, and the 'perceptual error'

function $g(p|q)$. As an illustrative example, we will assume that quality is evenly distributed between 0 and 1, i.e.

$$f(q) = \begin{cases} 1 & \text{if } 0 \leq q \leq 1 \\ 0 & \text{otherwise} \end{cases} \tag{5a}$$

(other distributions yield qualitatively similar results), while $g(p|q)$ is given by

$$g(p|q) = \frac{1}{a}\exp\left[\frac{-2|p-q|}{a}\right] \tag{5b}$$

The parameter a determines the degree of error in female assessment. At one extreme, as a tends to 0, assessment becomes perfectly error free, so that perceived quality is always identical to true quality and females always choose the best male on a lek. At the other extreme, as a tends to infinity, the degree of error is such that choice becomes entirely random. For intermediate values, females are more likely to prefer a high-quality to a low-quality mate, but do not always make the correct decision. This is illustrated in Fig. 1, which shows (for several different values of a) the probability that a female given a choice between two males will favour one over the other, as a function of the difference in quality between them.

Combining Eqs. 4 and 5, we have obtained explicit analytical expressions for the expected mating share of males of different ranks on leks of different sizes, as a function of a, the degree of error in female assessment. Since these expressions are complex, we do not give them here, but present the results graphically. Figure 2 shows the expected share of matings obtained by the best six males on a lek of size 12 as a function of a. The best male clearly gains fewer matings as the degree of error is increased. For the second-ranking male, however, expected mating share initially grows rapidly as a is increased from 0, but then levels off and begins to fall. The peak (at $a = 0.210$) reflects the fact that at intermediate levels of error, females do not all choose the best male (as is the case when $a = 0$), but there is still sufficient discrimination for the second-ranking competitor to receive a larger share of the matings than lower-ranked individuals on the lek (as a tends to infinity, the mating shares of all the males even out). The expected mating share of successively lower ranked males peaks at successively greater values of a, and for those of sufficiently low rank increases monotonically with the level of assessment error.

It is clear from Fig. 2 that the predicted distribution of matings is more uneven when the degree of error in female assessment is low. To quantify this trend, and to compare the effects of perceptual error on leks of different sizes, we can make use of the skew index, defined as the ratio of observed to maximum possible variance in mating share among the males on a lek (Keller and Reeve 1994; Keller and Vargo 1993; Reeve and Ratnieks 1993). Figure 3 shows this index as a function of a, the degree of error, for several different sizes of lek. Because we are concerned with the extent of skew in the expected
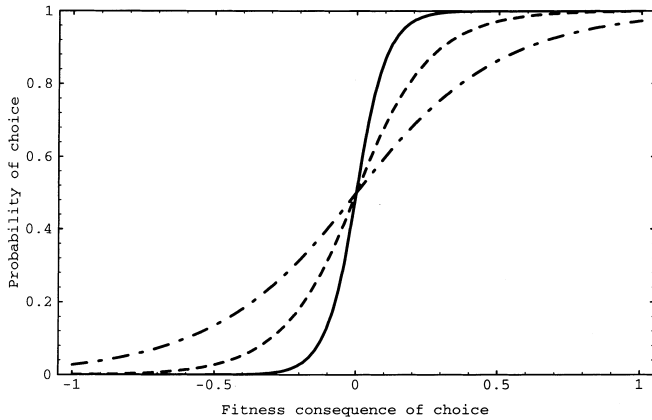
Fig. 1 The probability that a female will choose one male over another as a function of the fitness consequences of doing so (i.e. as a function of the mating value of the male in question relative to the value of his competitor), for different values of a, the degree of error in female assessment. The *solid line* gives the probability of choice for $a = 0.1$, the *dashed line* for $a = 0.25$, and the *dot-and-dashed* line for $a = 0.5$
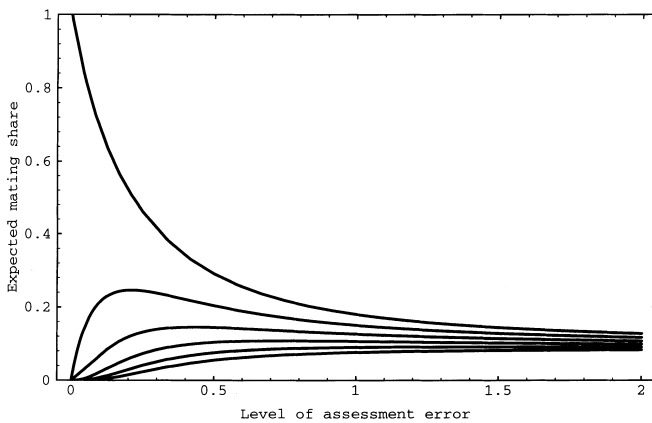

Fig. 2 Expected share of matings obtained by the six best males on a lek of size 12, as a function of a, the degree of error in female assessment. The top line is the mating share of the male who is ranked first in terms of quality, while successively lower curves give the mating share of successively lower-ranked males

distribution of mating shares, which can be precisely calculated using Eqs. 1 and 2, it is not necessary to correct the skew index for random variation as would be the case with empirical data (see Keller and Krieger 1996; Mackenzie et al. 1995b; Sutherland 1987). The figure reveals that for any given lek size, the degree of male mating skew decreases as the level of assessment error increases. The effects of error, however, are much greater on larger leks, so that for any given degree of error (greater than zero), the mating skew decreases as lek size increases. This effect is most marked for intermediate levels of error, since as a tends to infinity, skew tends to 0 regardless of the number of males present [qualitatively similar results are obtained using other measures of skew, such as Kokko and Lindström's (1997) index λ, obtained by fitting a geometric distribution to the observed pattern of matings].
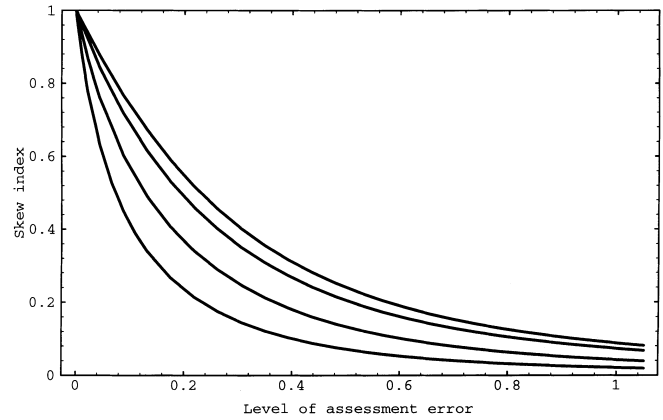

Fig. 3 Skew index of the expected distribution of matings on leks of different sizes, as a function of a, the degree of error in female assessment. The top line is the skew on a lek of size 2, while successively lower curves give the skew on leks of size 4, 8 and 16, respectively

The allotment of matings predicted by the model closely approximates a geometric distribution (although it is not exactly geometric). This is illustrated in Fig. 4, which shows the distribution of matings on leks of size 4 and 12, for low and for high levels of assessment error. Not only does the figure reveal the close approximation to a geometric distribution, it also highlights the greater impact of assessment error on larger leks: at the higher level of error, the best male is still predicted to claim well over half of all matings on a lek of size 4, while on a lek of size 12, his mating share is predicted to fall below 30%.

Discussion

Theories of the evolution of lekking are strongly dependent on the assumptions made about the degree of male mating skew and how this varies with lek size (e.g. Kokko and Lindström 1996; Widemo and Owens 1995). There have, however, been few attempts to model the consequences of imperfect female choice tactics for the distribution of matings on leks of different sizes. Bradbury et al. (1985) presented results of a simulation of imperfect choice, in which sets of male qualities were randomly generated, and a series of females was allowed to sequentially compare these and make a choice for mating (note that their model assumed a slightly different choice procedure to the present analysis). A simulation-based approach, however, allows one to calculate solutions for only a few sets of parameter values. The present model, by contrast, yields precise analytical expressions for the expected mating share of each male on a lek as a function of the degree of error, for leks of any given size.

The results of the model show that assessment error has, unsurprisingly, a strong effect on the level of skew in expected male mating success. The greater the degree of error, the lower the unanimity of female choice, and
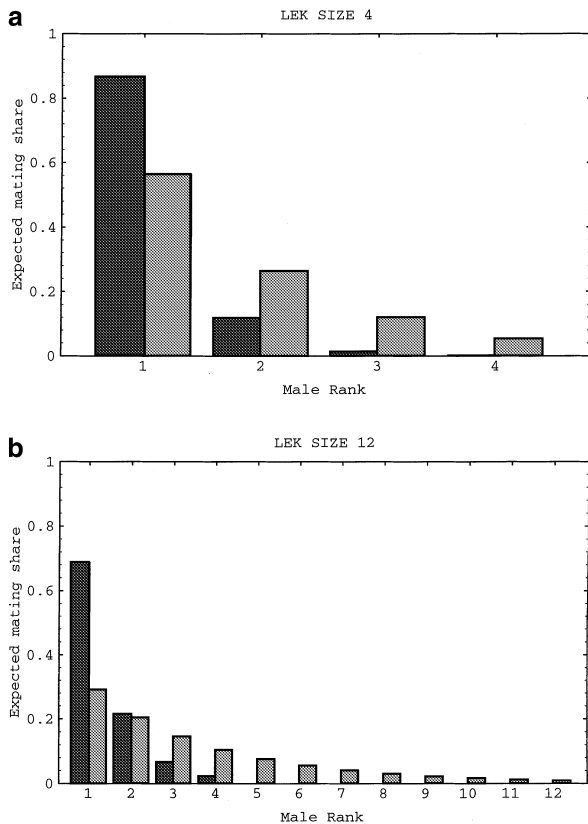
a

b

Fig. 4 Expected mating share of males of different quality ranks on leks of size 4 (**a**) and 12 (**b**), for low ($a = 0.1$, *black bars*) and high ($a = 0.5$, *stippled bars*) levels of assessment error

hence the lower the level of skew. This is disadvantageous for the best male on a lek, who obtains more matings the more accurately females can determine his status, but advantageous for low-ranking males who can only hope to obtain matings through assessment error. Intriguingly (as illustrated in Fig. 2), males who are of high rank but not the most desirable on the lek may do best at intermediate levels of error, since the top-ranked male does not then claim all the matings, but assessment is still sufficiently accurate for females to discriminate between high-ranking and low-ranking individuals.

More surprising than the negative relationship between assessment error and skew in expected male mating success is the fact that this effect is much more pronounced on larger leks. The explanation for this is simple. The more males that are present, the smaller the expected quality difference between competitors of adjacent ranks, and hence the harder it is to discriminate between them. On a small lek of 3 or 4 males, there are likely to be major differences in quality between the few individuals present, which are readily detectable even when assessment is strongly error prone. On a large lek of 15 or 20 males, by contrast, the best male is likely to be much closer in quality to lower-ranked competitors, so that even a small degree of inaccuracy in female choice may have a significant impact on the distribution of expected male mating success (although a female can

still expect, on average, to obtain a better-quality mate on a larger lek).

The chief consequence of the above is that for the same (non-zero) degree of error, mating skew should be lower on larger leks. Since, in reality, a degree of error is inevitable (see Getty 1996; Johnstone 1997; Luttbeg 1996; Sullivan 1994), this trend is likely to be universal. It may therefore be unnecessary to invoke increased levels of male aggression to explain the lower skew observed on larger leks, as previous studies have done (Alatalo et al. 1992; Höglund et al. 1993; Widemo and Owens 1995), since imperfect choice can also produce this pattern.

We have emphasized the qualitative pattern of results rather than quantitative predictions about the degree of male mating skew, because there are little data at present regarding the accuracy of female assessment relative to the degree of variation in male quality. Bradbury et al. (1985) argued, on the basis of their simulation results, that observed levels of variation in individual male display traits were insufficient to explain the observed skew in mating success, assuming 'reasonable' levels of assessment error. However, even ignoring the difficulty of deciding what constitutes reasonable error, female choice may often be based on multiple aspects of male display, which would allow for much more accurate assessment of mate quality than would be suggested by the variation observed in any one trait (Andersson 1989, 1993; Zuk et al. 1990, 1992; and see e.g. Collins et al. 1994; Iwasa and Pomiankowski 1995; Johnstone 1996). While quantitative predictions about the absolute level of male mating skew are therefore fraught with doubt, the predicted negative relationship between lek size and skew is insensitive to both the precise degree of assessment error and the distribution of male qualities.

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