

Comparing measures of breeding inequality and opportunity for selection with sexual selection on a quantitative character in bighorn rams

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Abstract

The reliability and consistency of the many measures proposed to quantify sexual selection have been questioned for decades. Realized selection on quantitative characters measured by the selection differential i was approximated by metrics based on variance in breeding success, using either the opportunity for sexual selection I_s or indices of inequality. There is no consensus about which metric best approximates realized selection on sexual characters. Recently, the opportunity for selection on character mean OSM was proposed to quantify the maximum potential selection on characters. Using 21 years of data on bighorn sheep (*Ovis canadensis*), we investigated the correlations between seven indices of inequality, I_s , OSM and i on horn length of males. Bighorn sheep are ideal for this comparison because they are highly polygynous and sexually dimorphic, ram horn length is under strong sexual selection, and we have detailed knowledge of individual breeding success. Different metrics provided conflicting information, potentially leading to spurious conclusions about selection patterns. I_δ , an index of breeding inequality, and, to a lesser extent, I_s showed the highest correlation with i on horn length, suggesting that these indices document breeding inequality in a selection context. OSM on horn length was strongly correlated with i , I_s and indices of inequality. By integrating information on both realized sexual selection and breeding inequality, OSM appeared to be the best proxy of sexual selection and may be best suited to explore its ecological bases.

Introduction

Sexual selection hinges on the differences in breeding success among individuals competing for access to mates (Darwin, 1871; Andersson, 1994) and drives the evolution of heritable characters that influence mating competitiveness. The relationship between phenotype and breeding success therefore determines the shape, direction and intensity of sexual selection (Price, 1970; Lande & Arnold, 1983). To understand sexual selection, it is important to quantify the covariance between

secondary sexual characters and breeding success. To that end, different metrics have been developed, but their reliability and consistency have been questioned for decades (Sutherland, 1985; Downhower *et al.*, 1987). Recently, the empirical and theoretical foundations of these metrics have been the subject of intense debate (Klug *et al.*, 2010; but see Krakauer *et al.*, 2011; Gowaty *et al.*, 2012; Jennions *et al.*, 2012).

The measurement of selection on quantitative characters requires individual-based data on both phenotype and breeding success. The selection differential and gradient estimate realized selection on a character by quantifying the covariance between character values and breeding success (Price, 1970). They represent the difference in mean character value between the entire population and individuals that reproduce (Lande &

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Arnold, 1983). Information on both individual phenotype and breeding success, however, is difficult to obtain in nature, especially for promiscuous and polygynous species where mating behaviour is not necessarily strongly correlated with breeding success (Coltman *et al.*, 1999). In the absence of individual-based data, population-level measures based only on the variance in reproductive output and irrespective of phenotype (Wade, 1979) have been used to assess the strength of sexual selection (e.g. Vanpé *et al.*, 2007). The opportunity for selection I and the opportunity for sexual selection I_s are based on the variance in relative reproductive or mating success, respectively, and are assumed to set the upper limit to the intensity of directional selection.

The opportunity for sexual selection I_s is rooted in the evolutionary framework of sexual selection, but its interpretation has been criticized (Klug *et al.*, 2010; but see Krakauer *et al.*, 2011; Jennions *et al.*, 2012). Assuming total heritability of fitness, the response to selection should equal the covariance of fitness with itself, and the intergenerational change in mean fitness would equal the variance in fitness (Crow, 1958; Arnold & Wade, 1984). The intergenerational change in mean fitness relative to the fitness of the population before selection corresponds to the variance in relative fitness, which is the opportunity for selection I , and mathematically describes Fisher's (1930) fundamental theorem of natural selection. Recent simulations, however, showed that the opportunity for sexual selection I_s was only weakly correlated with selection on quantitative characters (Klug *et al.*, 2010). Two main reasons may explain this inconsistency. First, I_s is based on the variance of mating success, which can be strongly affected by demographic fluctuations in adult sex ratio or sex-specific mortality (Sutherland, 1985; Koenig & Albano, 1986; Downhower *et al.*, 1987; Jennions *et al.*, 2012). The opportunity for sexual selection I_s may thus not correlate with realized sexual selection when mating success is affected by stochastic ecological factors (Klug *et al.*, 2010). Second, I_s does not take into account variance in quantitative characters; therefore, it cannot be used to study selection on particular characters (Klug *et al.*, 2010). Pelletier & Coulson (2012) developed a method to measure the maximum potential selection intensity on a quantitative character, called the opportunity for selection on a character mean (*OSM*). *OSM* is an extension of Lande & Arnold (1983)'s method, focusing on the covariance between a character and fitness and is thus calculated on the same scale as the sexual selection differential. It can estimate how the maximum potential selection on particular characters responds to ecological changes, contrary to I_s .

Several measures of inequality have also been proposed to assess the patterns and levels of sexual selection in nature. For example, a handful of experimental

studies showed that I_s increases with the operational sex ratio (OSR), defined as the relative numbers of females and males ready to mate at a given time and place (Jones *et al.*, 2004, 2005; Mills *et al.*, 2007). These studies manipulated OSR to impact sexual selection intensity. They assumed that OSR was an ecological determinant of mating competition, likely to influence mating inequality and sexual selection patterns. Recent studies, however, questioned the usefulness of OSR to quantify mating competition or the strength of sexual selection (Fitze & Le Galliard, 2008; Klug *et al.*, 2010; Kokko *et al.*, 2012). Partly because very few comparable studies exist (Jones *et al.*, 2002, 2005; Mills *et al.*, 2007; Fitze & Le Galliard, 2011), whether or not proxies of sexual selection correlate with realized sexual selection on characters remains controversial.

Proxies of sexual selection should correlate with the strength of sexual selection. A system under strong realized sexual selection on phenotype would thus provide a robust framework to test the reliability of proxies of sexual selection. We investigated the correlation between seven indices of mating inequality, I_s , *OSM* and the sexual selection differential on horn length of bighorn rams (*Ovis canadensis*). Bighorn sheep are ideal for such a comparative study: they are highly polygynous and sexually dimorphic, mate monopolization is strong, and ram horns are under strong sexual selection, their size being correlated with breeding success (Coltman *et al.*, 2002). Horn size also affects the acquisition of social rank (Martin *et al.*, 2013) which determines the mating tactic used by each ram (Hogg, 1984). Based on these observations, indices of mating inequality were predicted to correlate with the opportunity for sexual selection I_s , the opportunity for selection *OSM* on horn length and the sexual selection differential i on horn length. We used 21 years of individual-based monitoring and molecular assignment of paternities in a wild population of marked bighorn sheep to test this prediction.

Materials and methods

Study population and mating system

We used data collected during the ruts of 1988–1992 and 1996–2011 from marked and known-age bighorn sheep on Ram Mountain (52°N, 115°W, elevation 1080–2170 m), Alberta, Canada. Sheep of this population have been captured in a corral trap baited with salt since 1971 (Jorgenson *et al.*, 1993) and marked with unique combinations of ear tags and collars.

The rut is in late November and early December (Pelletier, 2005), and variability in ram breeding success arises partly from the use of alternative mating tactics (Hogg, 1984, 1987). Rams establish a linear dominance hierarchy where rank increases with age, horn size and body mass (Pelletier & Festa-Bianchet, 2006; Martin

et al., 2013). Rams in the top 1–4 ranks of the hierarchy obtain about 60% of paternities (Hogg & Forbes, 1997) using a mate guarding tactic called tending (Hogg, 1984). The remaining 40% of paternities are shared by up to three dozen subordinate rams that use alternative tactics.

Morphological measurements

Over 90% of adult rams were caught 1–3 times each summer. We measured total horn length of captured rams from the base to the tip, along the outer curvature. We accounted for summer growth by adjusting horn length to September 15, consistent with previous studies (Festa-Bianchet *et al.*, 2000). We estimated individual horn growth rates by fitting linear mixed models on repeated measurements each summer (Martin & Pelletier, 2011). Models included male identity as random intercept, the square root of capture date as random slope, and age and the square root of date as fixed effects. The square-root transformation of capture date linearizes growth over the summer (Festa-Bianchet *et al.*, 1996).

Paternity assignments and breeding success

Tissue sampling began in 1987. Samples were genotyped at 26 microsatellite loci (Coltman *et al.*, 2005), and we assigned 229 paternities among 61 males from 1988 to 1992 and from 1996 to 2011 with 95% confidence in CERVUS (Marshall *et al.*, 1998). Tissue samples were not collected in 1994–1996. Consequently, we excluded from analyses ruts from 1993 to 1995 because paternities for lambs conceived during these three ruts could only be established if they survived to 1997. Paternities of lambs that died before capture were unknown. Given that bighorn ewes produce only one lamb per year, the number of offspring assigned to each male during a rut was the genetic mating success, hereafter called breeding success.

We determined which females gave birth following a focal rut through udder examination at first capture the following spring, typically in late May. Neonatal lamb mortality was quantified by the number of lactating females not accompanied by a lamb and averaged 20% over the years considered here. Total lamb mortality was 30% before tissue sampling. Martin *et al.* (2014) showed that only lamb viability from weaning to 1 year of age influenced selection intensity on rams' phenotype. Therefore, we assume that early mortality did not bias our measure of selection on horn length.

Measures of breeding inequality

We calculated seven commonly used indices of inequality in resource acquisition (Kokko *et al.*, 1999) for

annual breeding success. Increasing values of these indices indicate greater inequality. In the following formulae, N is the number of rams, x and \bar{x} are breeding success and its mean, respectively, and σ^2 is the variance of breeding success. The equation for each index is followed by parentheses with the minimum value when success is equally distributed among males (Eq) and the maximum value when breeding is monopolized by one individual (Mo). Ra is the value when success is randomly distributed, for indices for which it can be computed.

The weighted skew index S (Keller & Vargo, 1993; Reeve & Ratnieks, 1993) describes the variance in breeding success among successful breeders, weighted by the number of competitors. $S = \frac{N_b^2 \sigma_b^2 + N_n}{N_b + N_n}$ ($Eq = 0$, $Mo = 1$), where N is the number of individuals, σ^2 is the sample variance in breeding success, and b and n refer to successful and unsuccessful breeders, respectively.

The corrected skew index S_c (Keller & Krieger, 1996) corrects potential bias in the S index due to random variation in breeding success (Tsuji & Tsuji, 1998) by the expectation of S under the hypothesis of random mating H_0 : $S_c = \frac{S - E[S|H_0]}{1 - E[S|H_0]}$ ($Eq = -\frac{S - E[S|H_0]}{1 - E[S|H_0]}$), $Ra = 0$, $Mo = 1$.

The linear skew index S_3 (Pamilo & Crozier, 1996) corrects for mathematical issues of S and does not require separation of successful and unsuccessful breeders. $S_3 = \frac{N-1/\sum_{i=1}^N (x_i/\sum_{i=1}^N x_i)^2}{N-1}$ ($Eq = 0$, $Mo = 1$), where $x_i/\sum_{i=1}^N x_i$ is the proportional breeding success of the i th individual across all individuals.

The monopolization index Q (Ruzzante *et al.*, 1996) estimates the observed degree of inequality in breeding success relative to when success is monopolized by one individual. $Q = \frac{\sigma^2 - x}{N\bar{x}^2 - x}$ ($Eq = -\frac{1}{N\bar{x}-1}$, $Ra = 0$, $Mo = 1$).

The iterative skew index λ (Kokko & Lindström, 1997) is an estimated parameter of a geometrical model of breeding success that fits the observed data. The expected proportion of breeding success p of an individual with rank r out of n males is: $[p_r] = \frac{\lambda(1-\lambda)^{r-1}}{1-(1-\lambda)^n}$ ($Eq=Ra=0$, $Mo=1$). Rank r is based on breeding success.

The Morisita index I_δ (Morisita, 1962) was initially developed to quantify spatial crowding. It was later proposed to measure breeding inequality (Tsuji & Tsuji, 1998). $I_\delta = N \frac{\sum_{i=1}^N x_i^2 - \sum_{i=1}^N x_i}{(\sum_{i=1}^N x_i)^2 - \sum_{i=1}^N x_i}$ ($Eq = 1 - \frac{N-1}{N\bar{x}-1}$, $Ra = 1$, $Mo = N$).

The binomial skew index B (Nonacs, 2000) estimates the difference between the observed variance in breeding success and the expected variance when all individuals have the same probability to reproduce. $B = \sum_{i=1}^N \left(p_i - \frac{n_i}{N}\right)^2 - \frac{1-(1/\bar{N})}{\sum_{i=1}^N x_i}$ ($Eq = \frac{1/\bar{N}-1}{\sum_{i=1}^N x_i}$, $Ra = 0$, $Mo = 1 - 1/N + \frac{1/\bar{N}-1}{\sum_{i=1}^N x_i}$).

Measures of opportunity for sexual selection

The opportunity for sexual selection I_s (Crow, 1958; Wade, 1979) is an indirect measure of selection because it does not consider selection on particular characters. I_s is the squared coefficient of variation in breeding success: $I_s = \frac{\sigma^2}{\bar{x}^2}$, where σ^2 and \bar{x} are the variance and mean of breeding success x . As I_s is the squared coefficient of variation of breeding success, it is also an index of inequality.

The opportunity for selection on a character mean OSM (Pelletier & Coulson, 2012) measures the maximum potential selection on particular characters. It is a sexual selection differential on ranked values of character z and fitness w : $OSM = cov(z_r, w_r)$, where fitness and character values are associated according to their rank.

Measures of selection

The sexual selection differential i (Lande & Arnold, 1983) assesses selection on a character by estimating the covariance between that character z and breeding success w_b : $i = cov(z, w_b)$. We estimated annual standardized sexual selection differentials on horn length by regressing annual relative breeding success against annual standardized horn length (Lande & Arnold, 1983). Relative breeding success was obtained by dividing each individual's absolute success by the annual mean. Horn length was annually standardized to zero mean and unit variance. Statistical significance for each sexual selection differential was estimated with generalized quasi-Poisson linear models where unstandardized characters were regressed against absolute fitness. Sexual selection differentials are expressed as the change in relative breeding success resulting from a change of one standard deviation in a character.

The realized proportion of achievable selection R_p (originally Q , Pelletier & Coulson, 2012) estimates realized selection on a character relative to the maximum potential selection on it. $R_p = \frac{i}{OSM}$ where i is the sexual selection differential and OSM is the opportunity for selection on a character mean. Given that the sexual selection differential i and OSM are defined on the same scale, as R_p approaches 1, more of the maximum potential for selection OSM is realized.

Statistical procedures

Skew indices were estimated using Skew Calculator (Nonacs, 2003, available at <https://www.eeb.ucla.edu/Faculty/Nonacs/PI>). All other statistics were performed with R version 2.14.1 (R Development Core Team, 2011). As all metrics of breeding inequality and selection were calculated annually, sample size was 21, the number of years of data. An outlier value of OSM was removed. Pairwise associations between measures of selection and indices of inequality were tested with Pearson's product moment correlation. We compared correlations using the function 'paired.r' from the library 'psych'. To better interpret the correlation matrix of selection measures and proxies, we also characterized their relationships using a principal component analysis (PCA) performed with the library 'FactoMineR' (Husson *et al.*, 2013). Angles between vectors approaching 0° or 180° indicate stronger positive and negative correlations between vectors, whereas 90° indicates no relationship.

Results

The median and mean values of the sexual selection differential i on horn length were 0.84 and 0.80, those of the OSM on horn length were 1.38 and 1.4, and those for the realized proportion of achievable selection R_p on horn length were 0.68 and 0.61 (Fig. 1). The median sexual selection differential i was four times stronger than the absolute median directional sexual selection differential of 0.21 for fecundity selection estimated as the number of offspring produced reported by Hereford *et al.* (2004). Along with high R_p , this result confirms that horn length of bighorn rams is under very strong sexual selection. The sexual selection differential i was only correlated with the OSM ($r = 0.53$, $P = 0.016$), contrary to the predicted correlation between the opportunity for sexual selection and sexual selection differential in species under strong sexual selection (Klug *et al.*, 2010). The OSM was also correlated with the opportunity for sexual selection I_s ($r = 0.63$, $P = 0.003$). The index I_s ($r = 0.42$, $P = 0.059$) and the opportunity for sexual selection I_s ($r = 0.36$, $P = 0.11$) were the proxies of sexual selection most

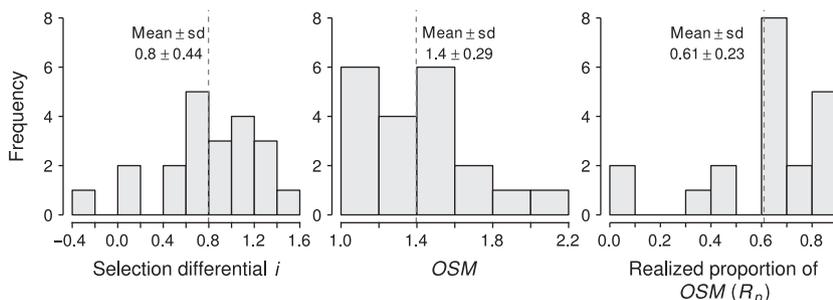


Fig. 1 Frequency distribution (number of years) of the sexual selection differential i , the opportunity for selection OSM and the realized proportion of achievable selection R_p . Calculated from the annual breeding success of bighorn sheep males at Ram Mountain, Alberta in 1988–1992 and 1996–2011.

strongly correlated with the sexual selection differential i , but these correlations were marginally not significant. Neither was a better correlate of i than the other ($t = 0.75$, $P = 0.46$). I_s was strongly correlated with all indices of breeding inequality (all P s < 0.026) except λ ($P = 0.56$, Table 1, Fig. 2). This correlation with S , S_c , S_3 and Q likely arises from the similarity in the calculation of these measures, which all rely on breeding variance. Accordingly, all indices of breeding inequality except λ correlated with each other (all $r > 0.47$, $P < 0.032$): the average correlation was 0.62 (CV = 0.37), or 0.72 (CV = 0.20) excluding λ . Despite this correlation among indices of inequality, and its correlation with I_s , OSM correlated with S , S_3 and I_δ , but not with S_c ($r = 0.41$, $P = 0.074$), Q ($r = 0.04$, $P = 0.851$) or B ($r = 0.08$, $P = 0.741$, Table 1). These results suggest that although OSM is a covariance-based measure of potential selection, it also adequately approximates breeding inequality.

The first three components of the PCA explained 89.83% of the variance (first = 59.12%, second = 21.03%, third = 9.67%, Table S1, Fig. S1). Two groups of variables can be distinguished in the PCA (Fig. 3). The first component pools the variance-based indices of breeding inequality. The second component, by definition independent of the first, synthesizes two opposed groups: the covariance-based selection measures (i and OSM) and λ . Therefore, measures of phenotypic selection may not be approximated by measures of breeding inequality.

Discussion

In a polygynous system with strong realized sexual selection, most proposed metrics of breeding inequality were not or weakly correlated with realized sexual selection. In particular, we found no correlation between the opportunity for sexual selection I_s and the sexual selection differential i . Our results suggest that the

opportunity for selection on a character mean (OSM) adequately quantifies both the maximum potential selection on a character and the variation in realized selection. A central concern about the opportunity for sexual selection is the expectation that a consistent proportion of maximum selection is realized (Klug *et al.*, 2010). On the contrary, we found that the yearly realized proportion of maximum achievable selection R_p on horn length was highly variable (CV = 0.38, Fig. 1), likely decoupling I_s and i in our study system. This is an important result because pronounced polygyny and strong sexual selection are two conditions under which a correlation between I_s and i was expected (Klug *et al.*, 2010).

The use of multiple measures of breeding inequality to study the multiple aspects of sexual selection has been promoted (Jones, 2009; Klug *et al.*, 2010). These measures are expected to covary because they share similar theoretical foundations but this assumption has rarely been tested. In addition, given that each index has its own specificities in describing breeding inequality (Kokko *et al.*, 1999), no *a priori* rule guides the choice of one over another. Sexual selection analyses, however, require an index correlated with measures of selection. The level of sexual selection we measured was $60.5 \pm 23.3\%$ of the maximum potential selection on horn length. This rate of realized sexual selection is higher than that reported for natural selection on juvenile body mass in wild red deer (*Cervus elaphus*, 36%) and feral Soay sheep (*O. aries*, 44%) in Pelletier & Coulson (2012). Horn length is therefore an appropriate trait to investigate the ability of various indices to estimate sexual selection in our system. The different proxies of sexual selection, however, provided conflicting information, with moderate correlations among indices of inequality. The PCA analyses revealed a relatively independent group of covariance-based selection measures, suggesting that measures of selection and of breeding inequality are not interchangeable. Thus, proxies of sexual selection based on breeding variance

Table 1 Correlation matrix [correlation coefficient (P -value)] for indices of mating inequality and measures of sexual selection on horn length.

S	1									
S_c	0.57 (0.007)	1								
S_3	0.96 (<0.001)	0.67 (0.001)	1							
Q	0.47 (0.032)	0.83 (<0.001)	0.63 (0.002)	1						
λ	0.15 (0.519)	0.3 (0.182)	0.29 (0.206)	0.72 (<0.001)	1					
I_δ	0.77 (<0.001)	0.81 (<0.001)	0.80 (<0.001)	0.66 (0.001)	0.24 (0.289)	1				
B	0.5 (0.022)	0.85 (<0.001)	0.66 (0.001)	1 (<0.001)	0.68 (0.001)	0.71 (<0.001)	1			
I_s	0.89 (<0.001)	0.62 (0.003)	0.87 (<0.001)	0.48 (0.026)	0.14 (0.559)	0.93 (<0.001)	0.53 (0.013)	1		
OSM	0.64 (0.003)	0.41 (0.074)	0.59 (0.006)	0.04 (0.851)	-0.22 (0.352)	0.54 (0.014)	0.08 (0.741)	0.63 (0.003)	1	
i	0.26 (0.254)	0.35 (0.120)	0.22 (0.330)	-0.04 (0.880)	-0.38 (0.093)	0.42 (0.059)	0.02 (0.946)	0.36 (0.106)	0.53 (0.016)	1
	S	S_c	S_3	Q	λ	I_δ	B	I_s	OSM	i

Calculated from the annual breeding success of bighorn sheep males at Ram Mountain, Alberta in 1988–1992 and 1996–2011. Significant correlations ($P < 0.05$) are in bold.

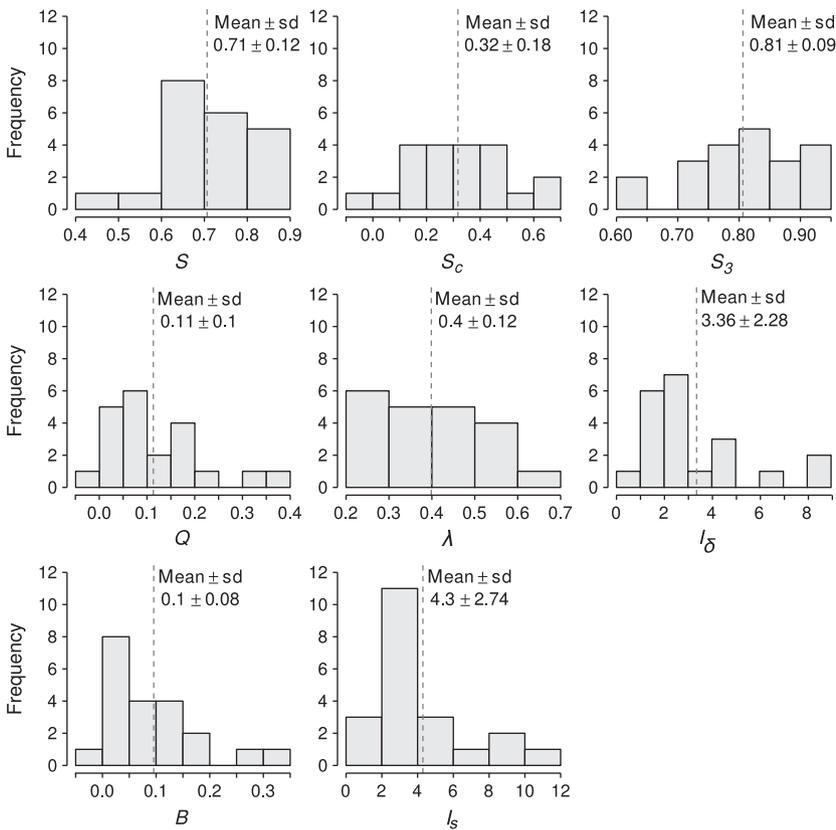


Fig. 2 Frequency distribution (number of years) of metrics of breeding inequality and maximum potential selection. Calculated from the annual breeding success of bighorn sheep males at Ram Mountain, Alberta in 1988–1992 and 1996–2011. S : weighted skew index, S_c : corrected skew index, S_3 : linear skew index, Q : monopolization index, λ : iterative skew index, I_δ : Morisita's index, B : binomial skew index, I_s : opportunity for sexual selection.

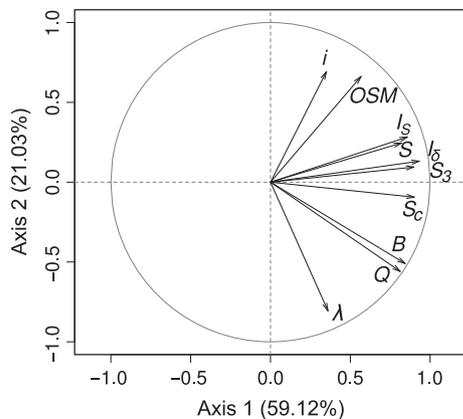


Fig. 3 Correlation circle from a PCA (axes 1 and 2) of different measures of selection on horn length and breeding inequality, for bighorn rams in 1988–1992 and 1996–2011, Ram Mountain, Alberta, Canada.

may not reliably estimate the strength of sexual selection in different mating systems.

Despite strong sexual selection on horn length, i was not correlated with I_s nor with any index of breeding inequality, although correlations with I_δ and λ were

nearly significant. The index λ tended to decrease; however, it was expected to increase with realized sexual selection. Accordingly, I_δ had the highest positive correlation with i and was strongly correlated with I_s . I_δ and I_s appeared to most reliably characterize patterns of mating monopolization. The correlations of OSM with i and I_s were similar ($t = 0.49$, $P = 0.627$), consistent with results for red deer and Soay sheep (Pelletier & Coulson, 2012). The OSM therefore integrated information provided by i , I_s and indices of breeding inequality. The OSM thus appears to be a reliable measure of potential selection because it links the approaches of the opportunity for sexual selection I_s and the character-centred sexual selection differential i . In contrast, the poor correlation of I_s with i supports the caution urged by Klug *et al.* (2010) concerning the use of I_s to draw conclusions about sexual selection.

Krakauer *et al.* (2011) defended the usefulness of I_s for the study of sexual selection because studying the effects of ecological factors on fitness variance is a central challenge in evolutionary ecology. Although our results confirm that breeding variance does not equal sexual selection, one could still argue that variance-based indices of inequality may help understand ecological factors affecting breeding variance. When phenotypic data are not available, such indices may

indeed describe and compare competitive contexts, like I_s and I_δ in this study. The value of I_s and I_δ , as descriptors of breeding inequality in a selection context, however, depends on the mean breeding success and the number of competitors. These are major drawbacks because these indices are sensitive to increasing variance in breeding success as its mean decreases (for details on mathematical limitations beyond the scope of our article, see Tsuji & Tsuji, 1998; Fairbairn & Wilby, 2001; Nonacs, 2003, 2000). This makes them nonindependent of ecological factors such as population size or number of competitors and critically limits their suitability to investigate the ecological drivers of breeding variance. Our results do not dispute, however, that the index I_δ and the opportunity for sexual selection I_s measure mating monopolization in polygynous species, as suggested by Jones *et al.* (2004, 2005) and Mills *et al.* (2007) for other taxa.

Multiple metrics commonly used to describe sexual selection may lead to different conclusions even when patterns of sexual selection are clear. Using an extensive data set of a strongly polygynous mammal in the wild, we provide empirical support to recent theoretical arguments concluding that proxies of sexual selection should be used with caution, especially when individual information on both phenotype and breeding success are not available. I_s and I_δ should be used carefully only to document breeding variance, and I_s should not be used as a proxy of the sexual selection differential but should be restricted to what it was designed for: characterizing mating systems (Arnold, 1994; Jones, 2009). The appeal of population-based metrics such as the opportunity for sexual selection is their theoretical ability to integrate breeding inequality in a selection context. Thus, to evaluate the intensity of sexual selection classical metrics such as selection differentials or gradients should be used by default, rather than multiply studies that summarize sexual selections with putatively integrative but unreliable metrics.

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References

- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.
- Arnold, S.J. 1994. Bateman's principles and the measurement of sexual selection in plants and animals. *Am. Nat.* **144**: S126–S149.
- Arnold, S.J. & Wade, M.J. 1984. On the measurement of natural and sexual selection: theory. *Evolution* **38**: 709–719.
- Coltman, D.W., Bancroft, D.R., Robertson, A., Smith, J.A., Clutton-Brock, T.H. & Pemberton, J.M. 1999. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Mol. Ecol.* **8**: 1199–1209.
- Coltman, D.W., Festa-Bianchet, M., Jorgenson, J.T. & Strobeck, C. 2002. Age-dependent sexual selection in bighorn rams. *Proc. R. Soc. B* **269**: 165–172.
- Coltman, D.W., O'Donoghue, P., Hogg, J.T. & Festa-Bianchet, M. 2005. Selection and genetic (co)variance in bighorn sheep. *Evolution* **59**: 1372–1382.
- Crow, J.F. 1958. Some possibilities for measuring selection intensities in man. *Hum. Biol.* **30**: 1–13.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. Murray, J, London, UK.
- Downhower, J.F., Blumer, L.S. & Brown, L. 1987. Opportunity for selection: an appropriate measure for evaluating variation in the potential for selection? *Evolution* **41**: 1395–1400.
- Fairbairn, D.J. & Wilby, A.E. 2001. Inequality of opportunity: measuring the potential for sexual selection. *Evol. Ecol. Res.* **3**: 667–686.
- Festa-Bianchet, M., King, W.J., Jorgenson, J.T., Smith, K.G. & Wishart, W.D. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. *Can. J. Zool.* **74**: 330–342.
- Festa-Bianchet, M., Jorgenson, J.T. & Réale, D. 2000. Early development, adult mass, and reproductive success in bighorn sheep. *Behav. Ecol.* **11**: 633–639.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford University Press, Oxford, UK.
- Fitze, P.S. & Le Galliard, J.-F. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. *Ecol. Lett.* **11**: 432–439.
- Fitze, P.S. & Le Galliard, J.-F. 2011. Inconsistency between different measures of sexual selection. *Am. Nat.* **178**: 256–268.
- Gowaty, P.A., Kim, Y.-K. & Anderson, W.W. 2012. No evidence of sexual selection in a repetition of Bateman's classic study of *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. USA* **109**: 11740–11745.
- Hereford, J., Hansen, T.F. & Houle, D. 2004. Comparing strengths of directional selection: how strong is strong? *Evolution* **58**: 2133–2143.
- Hogg, J.T. 1984. Mating in bighorn sheep: multiple creative male strategies. *Science* **225**: 526–529.
- Hogg, J.T. 1987. Intrasexual competition and mate choice in Rocky Mountain bighorn sheep. *Ethology* **75**: 119–144.
- Hogg, J.T. & Forbes, S.H. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk "unconventional" tactic. *Behav. Ecol. Sociobiol.* **41**: 33–48.
- Husson, F., Josse, J., Le, S. & Mazet, J. 2013. FactoMineR: Multivariate Exploratory Data Analysis and Data Mining with R.

- Jennions, M.D., Kokko, H. & Klug, H. 2012. The opportunity to be misled in studies of sexual selection. *J. Evol. Biol.* **25**: 591–598.
- Jones, A.G. 2009. On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution* **63**: 1673–1684.
- Jones, A.G., Arguello, J.R. & Arnold, S.J. 2002. Validation of Bateman's principles: a genetic study of sexual selection and mating patterns in the rough-skinned newt. *Proc. R. Soc. B* **269**: 2533–2539.
- Jones, A.G., Arguello, J.R. & Arnold, S.J. 2004. Molecular parentage analysis in experimental newt populations: the response of mating system measures to variation in the operational sex ratio. *Am. Nat.* **164**: 444–456.
- Jones, A.G., Rosenqvist, G., Berglund, A. & Avise, J.C. 2005. The measurement of sexual selection using Bateman's principles: an experimental test in the sex-role-reversed pipefish *Syngnathus typhle*. *Integr. Comp. Biol.* **45**: 874–884.
- Jorgenson, J.T., Festa-Bianchet, M. & Wishart, W.D. 1993. Harvesting bighorn ewes: consequences for population-size and trophy ram production. *J. Wildl. Manage.* **57**: 429–435.
- Keller, L. & Krieger, M.J.B. 1996. Mating success in male birds. *Nature* **380**: 208–209.
- Keller, L. & Vargo, E.L. 1993. Reproductive structure and reproductive roles in colonies of eusocial insects. In: *Queen Number and Sociality in Insects*, (L. Keller, ed.), pp. 16–44. Oxford University Press, Oxford.
- Klug, H., Heuschele, J., Jennions, M.D. & Kokko, H. 2010. The mismeasurement of sexual selection. *J. Evol. Biol.* **23**: 447–462.
- Koenig, W.D. & Albano, S.S. 1986. On the measurement of sexual selection. *Am. Nat.* **127**: 403–409.
- Kokko, H. & Lindström, J. 1997. Measuring the mating skew. *Am. Nat.* **149**: 794–799.
- Kokko, H., Mackenzie, A., Reynolds, J.D., Lindström, J. & Sutherland, W.J. 1999. Measures of inequality are not equal. *Am. Nat.* **72**: 358–382.
- Kokko, H., Klug, H. & Jennions, M.D. 2012. Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. *Ecol. Lett.* **15**: 1340–1351.
- Krakauer, A.H., Webster, M.S., Duval, E.H., Jones, A.G. & Shuster, S.M. 2011. The opportunity for sexual selection: not mismeasured, just misunderstood. *J. Evol. Biol.* **24**: 2064–2071.
- Lande, R. & Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.
- Marshall, T.C., Slate, J., Kruuk, L.E.B. & Pemberton, J.M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* **7**: 639–655.
- Martin, J.G.A. & Pelletier, F. 2011. Measuring growth patterns in the field: effects of sampling regime and methods on standardized estimates. *Can. J. Zool.* **89**: 529–537.
- Martin, A.M., Presseault-Gauvin, H., Festa-Bianchet, M. & Pelletier, F. 2013. Male mating competitiveness and age-dependent relationship between testosterone and social rank in bighorn sheep. *Behav. Ecol. Sociobiol.* **67**: 919–928.
- Martin, A.M., Festa-Bianchet, M., Coltman, D.W. & Pelletier, F. 2014. Sexually antagonistic association between paternal phenotype and offspring viability reinforces total selection on a sexually selected trait. *Biol. Lett.* **10**: 20140043.
- Mills, S.C., Grapputo, A., Koskela, E. & Mappes, T. 2007. Quantitative measure of sexual selection with respect to the operational sex ratio: a comparison of selection indices. *Proc. R. Soc. B* **274**: 143–150.
- Morisita, M. 1962. $I\sigma$ -Index, a measure of dispersion of individuals. *Res. Popul. Ecol.* **4**: 1–7.
- Nonacs, P. 2000. Measuring and using skew in the study of social behavior and evolution. *Am. Nat.* **156**: 577–589.
- Nonacs, P. 2003. Measuring the reliability of skew indices: is there one best index? *Anim. Behav.* **65**: 615–627.
- Pamilo, P. & Crozier, R.H. 1996. Reproductive skew simplified. *Oikos* **75**: 533–535.
- Pelletier, F. 2005. Foraging time of rutting bighorn rams varies with individual behavior, not mating tactic. *Behav. Ecol.* **16**: 280–285.
- Pelletier, F. & Coulson, T. 2012. A new metric to calculate the opportunity for selection on quantitative characters. *Evol. Ecol. Res.* **14**: 729–742.
- Pelletier, F. & Festa-Bianchet, M. 2006. Sexual selection and social rank in bighorn rams. *Anim. Behav.* **71**: 649–655.
- Price, G.R. 1970. Selection and covariance. *Nature* **227**: 520–521.
- R Development Core Team 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL <http://www.R-project.org/>.
- Reeve, H.K. & Ratnieks, F.L.W. 1993. Queen-queen conflicts in polygynous societies: mutual tolerance and reproductive skew. In: *Queen Number and Sociality in Insects*, (L. Keller, ed.), pp. 45–85. Oxford University Press, Oxford.
- Ruzzante, D.E., Hamilton, D.C., Kramer, D.L. & Grant, J.W.A. 1996. Scaling of the variance and the quantification of resource monopolization. *Behav. Ecol.* **7**: 199–207.
- Sutherland, W.J. 1985. Chance can produce a sex difference in variance in mating success and explain Bateman's data source. *Anim. Behav.* **33**: 1349–1352.
- Tsuji, K. & Tsuji, N. 1998. Indices of reproductive skew depend on average reproductive success. *Evol. Ecol.* **12**: 141–152.
- Vanpé, C., Kjellander, P., Galan, M., Cosson, J.F., Aulagnier, S., Liberg, O. et al. 2007. Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. *Behav. Ecol.* **19**: 309–316.
- Wade, M.J. 1979. Sexual selection and variance in reproductive success. *Am. Nat.* **114**: 742–747.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Correlation circles from a PCA (axes 1, 2, and 3) of different measures of selection on horn length and breeding inequality, for bighorn rams in 1988–1992 and 1996–2011, Ram Mountain, Alberta, Canada.

Table S1 Summary statistics of the PCA.

Data deposited at Dryad: doi:10.5061/dryad.vb73f.

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