Measuring sexual selection in mammals

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9   **Abstract**

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11   Sexual selection has been increasingly acknowledged as a major evolutionary driver in

12   many taxa. An unequal mating success arising through competition over mates is the

13   phenomenon that defines sexual selection. Therefore, demonstrating the presence of

14   sexual selection requires that the number or quality of mates are spread less evenly than

15   random processes would suggest. The objective of this study was to estimate the extent

16   of this inequality in male mammals by reviewing studies that measure variance in

17   genetic paternity. I found that few species showed high values of the standardised

18   variances in male reproductive success, I_m, and Nonacs's B indices. These species

19   differed from those with low or medium values in that, while in the latter the females

20   breed solitary, in the former, they are grouped for reproduction, which possibly

21   facilitates mate monopolization by males. Low levels of variance in reproductive

22   success could be explained because most species of mammals breed solitary or due to

23   high rates of extra-pair copulations by 'subordinate' males.

24

25   **Keywords:** Evolution, paternity, genetic reproductive success, breeding system, mating

26   system.

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Introduction

Sexual selection is considered one of the most pervasive forces that drive the evolution of reproductive traits in sexually reproducing organisms (Andersson, 1994). Darwin (1871) defined sexual selection as being dependent "on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" (p. 871). A modern definition proposes that sexual selection favours investment in traits that improve the likelihood of fertilization given limited access to opposite-sex gametes due to competition with members of the same sex (Jennions and Kokko, 2010). Sexual selection should be particularly intense in mammals because females bear most parental investment due to gestation and lactation, transforming them in a limiting resource for which males compete (Trivers 1972).

An unequal mating success that arises through competition over mates is the phenomenon that defines sexual selection (Arnold and Wade, 1984). Therefore, demonstrating the presence of sexual selection requires that the number or quality of mates are spread less evenly than random processes would suggest, in at least one of the sexes (Kokko et al., 2008). Kokko et al., (1999, p. 358) stated that, "unless the inequality itself can be shown to exist, and preferably measured and tested for significance, any further study of the causes behind it is fruitless".

In order to measure variance in mating success, a type of sexual selection index must be selected and the data that this type of index requires must be obtained. In the literature, there is a several indices (Klug et al., 2010, Anthes et al., 2017). Nevertheless, most indices correlate very strongly and measuring the same data with multiple indices will rarely reveal novel insights (Nonacs 2003). In this paper, I used the variance in relative reproductive success, the so called intensity (or opportunity) of sexual selection on males I_m, which is calculated as the variance divided by the square of the mean

53 (Arnold and Wade, 1984). I used I_m because it is the most common index used in

54 mammalian literature (Isvaran and Sankaran 2017). Based on the range shown for

55 mammalian species, Dubuc et al. (2014) considered values of $I_m < 1$ to show weak

56 opportunity for selection, values between 1 and 3 show moderate opportunity and

57 values of $I_m > 3$ show high opportunity for selection.

58   Ideally, data to measure sexual selection should be generated with an

59 experimental design that includes the entire reproductive period (Fritzche and

60 Booksmythe, 2013), because experiments can assess causal relationships (Anthes et al.,

61 2017). Clearly, this type of experiment is impossible to conduct with most mammals.

62 Thus, most of the classical studies in this taxon were conducted using behavioural traits

63 that are indirectly related to reproductive success, e.g. harem size (Emlen and Oring

64 1997). Using these behavioural surrogates, the overall result was that mammals showed

65 high skew in reproductive success (review, for example, in Clutton-Brock, 1988).

66 Recently, these measures have been replaced by estimations of paternity using genetic

67 techniques, which provides a valuable measure of the opportunity of sexual selection

68 because it excludes the possibility that males who are not dominant in direct

69 competition for mates may obtain extra-group copulations (Wade and Shuster, 2004).

70   The objectives of this work were: (i) to review the literature on genetic paternity

71 in mammals in order (ii) to obtain estimates of the opportunity of sexual selection in this

72 taxon, (iii) to compare genetic with behavioural measures of male reproductive success

73 and (iv) to discuss the role of sexual selection in mammalian evolution.

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75 **Methods**

76 *Creating datasets*

For paternity data, the methodology of Isvaran and Sankaran (2017) was adopted which aimed to isolate estimates of access to fertilization (i.e., the effect of sexual selection on variation in reproductive success) and remove the effect of factors related to viability selection (i.e., survival between breeding seasons and lifespan). A literature search was conducted for estimates of male genetic mating success, based on genetic measures of paternity (Supplementary Information 1). This search had four stages. In the first, I used two keywords in Google Scholar database, 'paternity' and 'mammal', to get a first list of articles. The second stage consisted of a review of those journals that appeared in the first stage, using the same two words in the search tools available in the web pages of the journals themselves. The third stage consisted of a review of the literature cited in all the articles obtained in the second stage. The fourth stage consisted of a review of the literature cited in all the articles obtained in the third stage. Only fieldwork studies were considered unless otherwise mentioned.

In order to obtain a measure of inequality in reproductive success, it was necessary to extract the information on paternity from each study. In all studies, paternity was established through the use of molecular markers and, in order to do so, skin or blood samples were taken from those parents and offspring that were captured and then the degree of kinship was determined. In most cases, male reproductive success was presented as the number of pups that were assigned to each sampled male. Therefore, I calculated the variance and the mean in male reproductive success of the total of the sampled males. In some cases, the variance and the mean were directly provided by the study. In studies that report male reproductive measures counted across multiple years, the annual mean number of offspring per male was obtained first, to then obtain the mean and variance for the total number of males.

Female breeding system data were obtained from Lukas and Clutton-Brock (2020). Information gaps were filled with information provided by the Animal Diversity Web, University of Michigan (https://animaldiversity.org/ accessed September - November 2020). Data on mating systems were obtained from the same sources of paternity data.

Measuring inequality in reproductive success

I used the 'opportunity of sexual selection' calculated as $I_m = var/mean^2$ of paternity data. I followed Dubuc et al. (2014)'s criteria to define low, medium and high skew in male reproductive success. Complementing and for comparison, I calculated the Nonacs' B index (Nonacs, 2000, 2003) using the program Skew Calculator 2003 (http://www.eeb.ucla.edu/Faculty/Nonacs/PI.html), which tests whether paternity distribution is different from that expected by chance. This program allows splitting into separate groups, but I did not so because only a few number of studies provided data by group. This program provides the following confidence intervals of B: (i) if they include zero, the distribution of benefits is not different from random chance; (ii) if the lower confidence interval includes the 'equal sharing' value (also provided), then an equal distribution of benefits cannot be excluded; (iii) if the intervals do not include zero, this indicates a skew distribution of paternity, with some males being significantly more successful than others; (iv) under the conditions of (iii), B values close to zero indicate low variance in mating success, while B values close to one indicates high levels of paternity monopolisation. Therefore, values < 0.5 were considered low skew values, and > 0.5 were considered high. I included studies that both sampled and not sampled unsuccessful males. This could affect the level of skew estimated with I_m but is more controlled by B.

126 *Relating variables*

127 All relationships were analysed employing the phylogenetic generalised least squares

128 (PGLS) method in R, so the phylogenetic signal could be controlled (Martins and

129 Hansen 1997). First, a simple regression was conducted to compare I_m with B, then a

130 multiple regression was conducted with I_m as a dependent variable (log transformed,

131 with five zero-data assigned a value of -2) and four independent variables: body size

132 (log transformed), sexual size dimorphism (log transformed) and two proxy measures of

133 strength of sexual selection, based on the intensity of the male competition for mates:

134 mating system (polygyny, polygynandry, monogamy) and female breeding system

135 (plural versus single breeders).

136

137 **Results**

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139 A dataset was built containing genetic variance information from a total of 158 mammal

140 species, of which 156 had data that allowed the estimation of I_m, and 126 had data that

141 allowed the estimation of B. Mean I_m and B were 1.48 (SD=2.04) and 0.027

142 (SD=0.098). As expected, I_m and B were strongly correlated (λ=0, r^2=0.22, $F_{1, 116}$=33.8,

143 p<0.001). According to the categorisation made by Dubuc et al. (2014), most species

144 showed weak selection opportunity (50.3%), while only 13.8% of species had high

145 levels of selection opportunity and 35.8% showed a moderate opportunity for sexual

146 selection (Figure 1). These frequencies showed statistically significant differences

147 (χ^2=32.2, gl=21, P<0.001). The B index showed a similar pattern (Figure 1), given that

148 the number of species with non-skewed (equal or random) distributions (59.1%) was

149 higher than the number of species with a skewness (χ^2=4.2, gl=1, P=0.04).

150   Four behavioural measures of sexual selection were compared with I_m (Table 1).

151   The only significant correlation was between I_m and the breeding system.

152

153   **Discussion**

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155   Results obtained in this study, which used the largest available dataset on genetic

156   measures of paternity variance in mammals, suggest low levels of opportunity of sexual

157   selection in this taxon. A possible explanation of these low values of genetic measures

158   of variance in reproductive success would be the effect of extra-group copulations. Most

159   mammalian species were described as behaviourally polygynous, with consequent

160   variance in the ability of males to monopolize females (Emlen and Oring, 1977). Large

161   males can monopolise females by contest competition, while small males can evolve

162   alternative reproductive tactics, such as sneak spawning (Jennions and Kokko 2010). If

163   extra-pair copulations are achieved by less successful males in direct competition, the

164   result is a decrease in the variance in male reproductive success. In populations with

165   more than one type of male reproductive tactic, it could be that ethological observations

166   indicate a high variance in reproductive success with large males gaining more mates

167   that small ones, but this does not necessarily imply a high paternity variance, since

168   alternative tactics could be equally effective but less conspicuous, with the consequent

169   homogenization of this variable. Under this hypothesis, sexual selection operates

170   maintaining equilibrium between two or more alternative reproductive strategies

171   depending on their size or age.

172   This hypothesis was partially tested by Isvaran and Sankaran (2017), who

173   showed that when breeding group sex ratios are strongly female-biased (highly

174   polygynous systems, multi-male systems with female-biased groups), extra-group

paternities appear to decrease variance in male reproductive success. These authors

described this result as 'an unsuspected relationship between overt (social mating

system) and covert (extra-group paternity) mating tactics and the potential for sexual

selection in male mammals'.

A correlation between breeding system and intensity of sexual selection was

found. This relationship is predicted by sexual selection theory, which postulates that

the extent to which breeding females aggregate affects mating competition (Emlen and

Oring, 1977). In plural breeding species, the number of potential breeding partners that

individual males can guard effectively is higher than in singular breeders, increasing

variance in male reproductive success (Kvarnemo and Ahnesjo, 1996). In most

mammalian species, females breed solitary (Lukas and Clutton-Brock 2020), therefore it

is expected relatively low levels of intensity of sexual selection in this taxon if sexual

selection increases with female group size.

Another hypothesis is that current variation in reproductive success refers only

to the maintenance of sexually selected traits, not their origin and further evolution in

the past, when variance in reproductive success might have been different (Grafen

1988). In other words, the trait would cause skewed reproduction among males, but

would quickly become fixed (Fisher's run-away model of sexual selection, Fisher 1930).

This study only analyses the current opportunity of sexual selection measured as

variance in parenting but does not say anything about the impact of sexual selection on

actual traits, such as sexual size dimorphism. Those traits need to be heritable and have

strong enough fitness advantages to show change in trait forms over evolutionary time.

Therefore, a future study should analyse the relationship between sexual traits and

paternity variance in mammals.

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210   201   **Acknowledgements**

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254 Table 1. Results of the phylogenetic generalised least squares using standardised

255 variance in male reproductive success I_m as dependent variable and four independent

256 variables: breeding and mating systems. The global analysis gave: $\lambda=0$, $r^2=0.08$, $F_{1,}$

257 $_{133}=2.94$, p=0.02

258

| Independent variable	Estimate	Std. Error	t-value	p-value
(Intercept)	-0.45	0.15	-30.8	0.0002
Body mass	0.01	0.04	0.14	0.89
Sexual dimorphism	0.43	0.40	1.06	0.29
Breeding system	0.33	0.11	29.4	0.003
Mating system	0.02	0.04	0.64	0.52

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260

280   261   Figure 1. Percentages of low, moderate and high values of standardised variance in male

281   262   reproductive success was calculated: I_m and Nonacs' *B* index. Low values of

282   263   opportunity of sexual selection were significantly more frequent than high values.

283   264 χ^2=32.2, gl=21, *P*<0.001
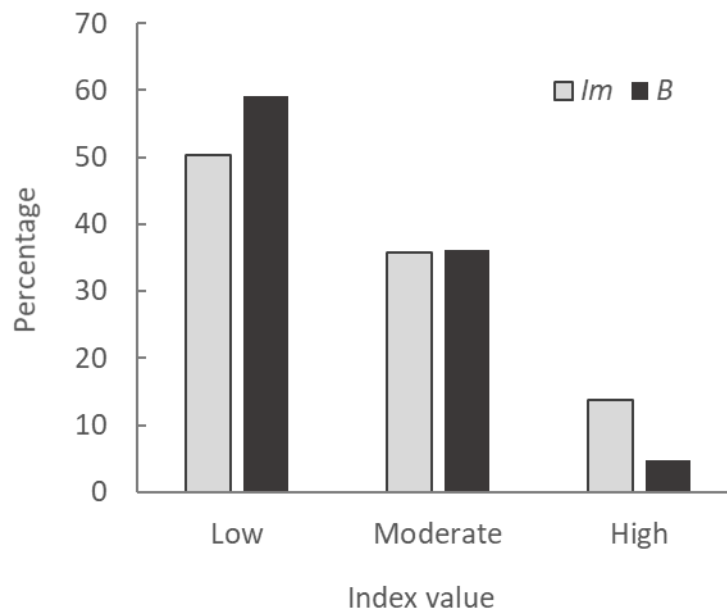
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Supplementary Online Material