



## Research Article

## Evolution of sexual size dimorphism in mammals: sexual or natural selection?

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**Abstract**

Sexual size dimorphism may have evolved through two processes: sexual or natural selection. The sexual selection theory states that males compete for mate monopolization and larger males can sire more offspring than smaller ones—factors that resulted in the evolution of sexual size dimorphism. An alternative hypothesis suggests that there was a change in ecological conditions (e.g., from close to open habitats that increased predation risk or a climatic change that increased thermoregulation requirements) that favoured an increase in body size that was more significant in males than in females. In the present study, phylogenetic confirmatory path analyses were conducted to test the hypotheses on the causal relationships between five characters: breeding system, sexual size dimorphism, body weight, daily activity (representing the initial change in habitat that induced female grouping), and mating system (monogamy and polygyny) or variance in genetic paternity (measures of intensity of sexual selection). The best-fit models in the path analyses assumed that dimorphism evolved through natural selection following the evolution of large body size, which in turn influenced the evolution of breeding groups and polygyny.

### Introduction

Sexual size dimorphism is the difference in body proportion between the sexes, which is generally represented as a ratio of male to female body weight (Fairbairn, 1997). Dimorphism in other features, such as teeth, horns, pelage or brain size, is typically a consequence of size dimorphism (Pérez-Barbería and Gordon, 2000; Plavcan, 2004). Understanding the evolutionary origin and adaptive significance of sexual size dimorphism is important for several scientific disciplines. For example, it can provide insights into the life history and behaviour of extinct species for palaeontologists and sex-related variations in humans, such as health, nutrition, and behaviour, for anthropologists and psychologists (Plavcan, 2011; Stulp and Barrett, 2016).

Sexual size dimorphism may have evolved through two processes: sexual or natural selection (Darwin, 1871; Slatkin, 1984; Plavcan, 2011). According to the sexual selection theory proposed by Darwin (1871), males compete for mate monopolization and larger males can sire more offspring than smaller males, which led to the evolution of sexual size dimorphism (Clutton-Brock, 1988; Andersson, 1994). An alternative hypothesis suggests that there was a change in ecological conditions (e.g., a change from close to open habitats that increased predation risk or a climatic change that increased thermoregulation requirements) that favoured an increase in body size that was less significant in females than in males (Slatkin, 1984; Plavcan, 2011). For example, Northern elephant seals (*Mirounga angustirostris*) are a frequently cited case of the role of sexual selection in the evolution of sexual dimorphism in body size: males evolved larger sizes than females because large males were more successful in competition for reproductive mates in a polygynous context (Le Boeuf, 1974). There is another hypothesis based on natural selection that proposes that the larger sizes of males are due to ecological pressures: a greater body mass implies greater fat reserves, which allows males to travel greater dis-

tances and thus reach the best but most distant foraging areas (Le Boeuf et al., 2000).

Under the natural selection hypothesis, at least four mechanisms were postulated to explain why males reached larger sizes than females. The first mechanism was proposed by Leutenegger and Cheverud (1985), who developed a quantitative genetic model that suggested that, if natural selection favors large body sizes, males will produce larger bodies than females as far as male sizes are more variable or less heritable than those of females. The other three mechanisms — competitive displacement, bimodal niches, and dimorphic niches — were proposed by Slatkin (1984). Niche partitioning between the sexes may occur when the sexes compete for resources such as food. In the bimodal niche model, both sexes have the same needs, and they could evolve to the same two optima. Dimorphic niches arise when there is a different optimum value of the trait in each sex due to intrinsic differences between males and females because of their different energetic needs to ensure successful reproduction or because of their different social roles (Slatkin, 1984).

To disentangle the effects of sexual and natural selection on the emergence of sexual dimorphism in mammals, it needs to be framed in a broader evolutionary context. Reconstruction of ancestral characters have indicated that the first mammals were nocturnal (Maor et al., 2017), relatively small (Baker et al., 2015), solitary (Lukas and Clutton-Brock, 2013), and monomorphic (artiodactyls: Janis, 1982, primates: Plavcan, 2001; pinnipeds: Krüger et al., 2014) and had a mating system based on male roaming and low levels of polygyny (Lukas and Clutton-Brock, 2013). Under these conditions, sexual selection is expected to be weak, since males were unable to monopolize receptive females that were evenly distributed in space (Emlen and Oring, 1977; Lukas and Clutton-Brock, 2020). While many extant species have retained these characteristics, some taxa, mainly primates, ungulates, and marine carnivores, have evolved towards diurnal life, large body size, sociality, sexual dimorphism, and high levels of polygyny (Ralls, 1977; Fairbairn, 1997; Weckerly, 1998).

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There is a consensus that a change in the activity pattern towards diurnality accompanied by an increase in predation risk induced the evolution of sociality and female breeding systems (Jarman, 1974; Wrangham, 1980; Shultz et al., 2011; Lukas and Clutton-Brock, 2020). It is also widely accepted that the number of potential breeding partners that individual males were able to guard effectively increased after female gregariousness evolved, facilitating the monopolization of many females by a dominant male; this amplified the intensity of sexual selection and promoted high levels of polygyny (Emlen and Oring, 1977; Alexander et al., 1979). This evolutionary path, which generated the conditions for sexual selection to operate (*habitat change* → *female grouping* → *polygyny*) is common to all the models on the evolution of sexual size dimorphism (Fig. 1), which are described in the subsequent paragraphs.

Sexual selection theory states that when the opportunity to monopolize female mates emerged, it was followed by male-male competition (Andersson, 1994). Larger males were more successful in male-male contests than smaller males, thereby siring more offspring and driving the evolution of sexual size dimorphism (Fig. 1a; Boness, 1991; Lindenfors and Tullbert, 1998; Loison et al., 1999; Pérez-Barbería et al., 2002; Bro-Jorgensen, 2007; Jones et al., 2009). An alternative version of the sexual selection model (Fig. 1b) was proposed to explain Rensch's rule, which states that male-biased size dimorphism increases with body size (Rensch, 1950). This alternative model suggested that body mass in males increased due to sexual selection, and females were expected to show a correlated low-intensity response due to reproductive constraints (Andersson, 1994; Fairbairn, 1997; Lindenfors et al., 2007, 2002; Gordon, 2006).

Another model proposed that sexual size dimorphism evolved through natural selection (Fig. 1c). This model possesses two evolutionary paths. The first one was already described: *habitat change* → *female grouping* → *polygyny*. In the second path, an increase in body size (due to ecological factors that differ between mammalian taxa: changes from closed to open environments in Artiodactyls (Jarman, 1974), from nocturnal to diurnal habits in primates (Leutenegger and Cheverud, 1985) or a decrease in sea temperature for pinnipeds (Krüger et al., 2014)) triggered the evolution of sexual size dimorphism. When males became substantially larger than females, the impact of sexual harassment on females is expected to be greater; thus, females aggregate to minimize this risk (Trillmich and Trillmich, 1984; Cassini, 2021), which in turn favoured the evolution of plural breeding females (Emlen and Oring, 1977; Cassini, 1999). In this model, sexual size dimorphism also influenced mating system by increasing intensity of male-male competition for mates. Large and small males probably entered the competitive arena with a predisposition for different reproductive tactics: large males monopolize females by contest competition, whereas small males evolved alternative reproductive tactics, such as sneak spawning (Arnold and Wade, 1984; Kokko and Jennions, 2008; Isvaran and Sankaran, 2017).

Finally, it is possible to build a fourth, combined model in which sexual size dimorphism evolved because of both natural and sexual selection, i.e., it evolved both because of an increase in body size due to changes in ecological conditions and because of an increase in female aggregation that facilitated male-male competition for mates (Fig. 1d). This combined model predicts that the strength of the causal link *habitat change* → *female grouping* → *polygyny* → *dimorphism* will have the same strength that the link *habitat change* → *body size* → *dimorphism*.

Confirmatory path analysis, a statistical technique that can evaluate and compare causal models using observational data (von Hardenberg and Gonzalez-Voyer, 2012; van der Bijl, 2018), can be used to disentangle the roles of sexual and natural selection in the evolution of sexual size dimorphism in mammals. This tool has great value for comparative biologists since they generally cannot gather experimental data on evolutionary hypotheses (Shipley, 2000). For understanding the evolution of sexual size dimorphism, path analysis can be used to determine whether this trait evolved because of male competition for mates or in response to an ecological pressure unrelated to reproduc-

tion (Gonzalez-Voyer and von Hardenberg, 2014). The objective of this study was to test different causal models that could explain the evolution of sexual size dimorphism in mammals, using phylogenetic confirmatory path analysis (Gonzalez-Voyer and von Hardenberg, 2014).

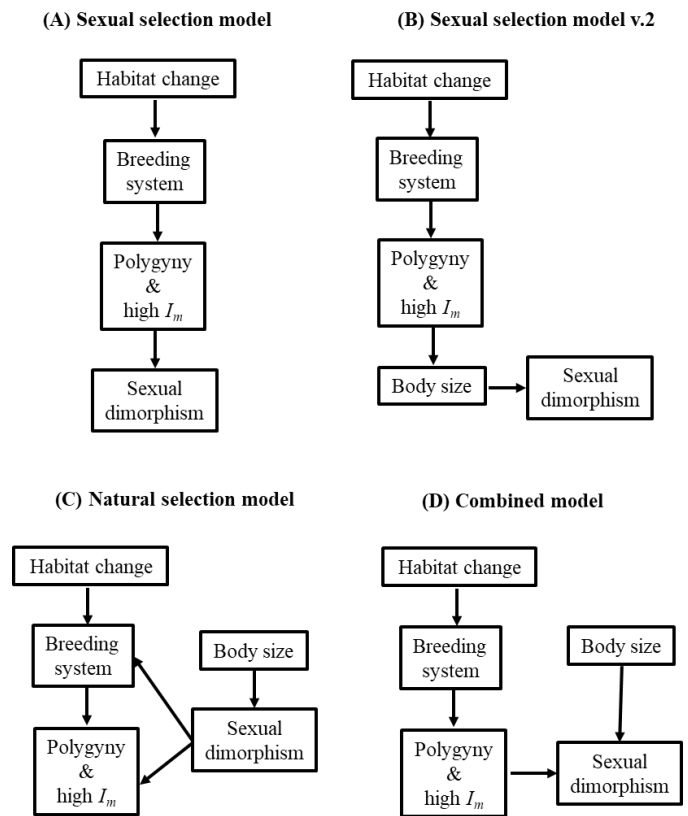


Figure 1 – Causal models of the evolution of mammalian traits, which are described in the Introduction.

## Methods

### Collecting datasets

Sexual size dimorphism was calculated as the ratio of male to female body weight, except for cetaceans, for which only total body length data were available for both sexes, thus ratio in length replaced ratio in weight in this taxon (body length strongly predicts body mass in cetaceans; Silva, 1998; Cranford, 1999). When evaluating the relationship between dimorphism and body size, it is indistinct to use female size, male size or the average (Smith, 1999; Gordon, 2006). Data on dimorphism and size were log transformed (following Smith, 1999) and were obtained from several sources for the mammalian orders artiodactyls (Pérez-Barbería and Gordon, 2000), primates (Gordon, 2006), cetaceans (Dines et al., 2015), and rodents (Schulte-Hostede, 2007), whereas they were obtained from PanTHERIA (Jones et al., 2009) and a raw database (<http://www.utheria.org> accessed April, 2015; Gonzalez-Suarez, pers. comm.) for the remaining species (detailed information in Supplement S1 and S2). Activity data were obtained from Maor et al. (2017), and the species were categorized as diurnal (species that are active only during daylight hours or during the day as well as night, as cathemeral species) or nocturnal (species that are active only at night). Breeding system data were obtained from Lukas and Clutton-Brock (2020), who categorized breeding system into two states: singular breeding systems, where breeding females normally occupy separate territories (solitary females) and plural breeding systems, where many breeding females normally aggregate in one territory (female groups).

The mating systems were classified in polygyny and monogamy (Lukas and Clutton-Brock, 2013). Assuming that sexual selection is more intense in a polygynous context than in monogamy, mating systems have been used as a measure of sexual selection intensity (e.g.,

Lindfors, 2002). Thirteen gaps in data on activity were filled with information from the Animal Diversity Web, University of Michigan (<https://animaldiversity.org> accessed September–November, 2020). The standardized variance in male reproductive success was calculated as (Arnold and Wade, 1984). Following Isvaran and Sankaran (2017), male genetic mating success was based on genetic measures of paternity, which aim to isolate estimates of access to fertilizations. For paternity data, a literature search was conducted to estimate male genetic mating success based on genetic measures of paternity (Supplement S2). Two keywords, 'paternity' and 'mammal' were used in Google Scholar and in the search tools available on the web pages of the most relevant journals. The reference lists of the selected papers were further analysed to search for additional impactful records. The search was terminated when the same sources were repeatedly found (Hagen and Kumschick, 2018). Activity, breeding system, and mating system were used as the categorical variables.

Finally, two datasets were built using five variables: breeding system, sexual size dimorphism, body weight, daily activity (representing the initial change in habitat), and mating system or  $I_m$  (Supplement S1). Thus, one dataset used the variable mating system and the other  $I_m$  (log transformed). The reason for using two different datasets is that behavioural and genetic data can produce different results in studies on sexual selection. In mammals, several studies showed the discrepancies between behavioural and genetic measures of fitness (Coltman et al., 1999; Young and Bennett, 2013; Cassini, 2020). An explanation for these discrepancies is that paternity analysis of offspring using molecular techniques rules out the possibility that apparently nonmating males are nevertheless successful in extra-group copulations (Wade and Shuster, 2004). The larger dataset, which used the data on mating systems, contained information of 843 species, whereas the smaller dataset contained genetic variance information of 144 mammal species that allowed the estimation of  $I_m$  (log-transformed to satisfy normality assumptions).

## Candidate models and phylogenetic trees

The candidate models were built following van der Bijl (2018), who advised against running excessive combinations and to build a set of models with the combinations that only described the different hypotheses for comparison. Therefore, only the four models described in Introduction (Fig. 1) were evaluated using both datasets.

Two phylogenetic trees were required, one for each dataset. They were constructed in the VertLife.org webpage. Two sets of 1000 trees were downloaded, and TreeAnnotator v1.10.4 in BEAST v1.4.4 was used to build two the consensus trees.

## Phylogenetic confirmatory path analysis

Classical regression analyses can provide information on the degree of statistical relationships between variables but cannot explain causal connections (Shipley, 2013). Therefore, a phylogenetic confirmatory path analysis was performed to build models of causal hypotheses among variables and test whether the data conformed to the causal model. Path analyses consider the non-independence of observations because of the phylogenetic relatedness among species (von Hardenberg and Gonzalez-Voyer, 2012). In structural equation models, causal relationships are translated into a set of linear equations that follow a causal structure (Gonzalez-Voyer and von Hardenberg, 2014). Shipley (2000) developed the d-separation method for path analysis, which specifies the minimum set of independent and conditionally independent relationships that holds true for all variables in a hypothesized causal model (Gonzalez-Voyer and von Hardenberg, 2014).

Shipley (2000) then proposed combining the  $p$ -values using Fisher's  $C$  statistic, which is calculated as  $C = -2 \sum_{i=2}^k (\ln(p_i))$ , where  $k$  is the number of conditional independencies in the minimum set and  $p$  is their  $p$ -value. The  $C$  statistic follows a  $\chi^2$  distribution, with  $df = 2k$ , thereby providing a method for determining the goodness of fit of the entire path model (Gonzalez-Voyer and von Hardenberg, 2014). As in any

Chi-Square Goodness of Fit Test, a significant  $p$ -value would indicate that the available evidence rejects the model.

More than one model can meet the requirement of a  $C$  statistic with  $p > 0.05$ , so Gonzalez-Voyer and von Hardenberg (2014) proposed a criterion similar to Akaike's information criterion (Akaike, 1974) called the  $C$  statistic information criterion, which is calculated as  $CICc = C + 2qx \frac{n}{(n-1-q)}$ , where  $q$  is the number of parameters estimated in the path model and  $n$  is the number of species (Cardon et al., 2011). Models can be ranked based on  $\Delta CICc$ . Generally, models with  $\Delta CICc < 2$  are considered to have substantial support (Burnham and Anderson, 2002). Finally,  $CICc$  weights ( $w$ ) provide a measure of the strength of the evidence (Burnham et al., 2011). Results from model selection should be interpreted in relative terms within the context of the set of tested models (Burnham et al., 2011).

I conducted phylogenetic path analyses using the `phylopath` package in R Software, which is a user-friendly program developed by van der Bijl (2018) ([https://cran.r-project.org/web/packages/phylopath/vignettes/intro\\_to\\_phylopath.html](https://cran.r-project.org/web/packages/phylopath/vignettes/intro_to_phylopath.html)).

This package follows the general approach to phylogenetic methods. I incorporated three elements into the program: a phylogenetic tree, the data, and the models of evolution (consensus phylogenetic tree and databases used in this study are detailed in Supplement S1 and S2). I incorporated four models (represented graphically in Fig. 1) to `phylopath` with the format:

```
<- define_model_set(
  Sexual1 = c(SSD~MS,MS~BS,BS~Act),
  Sexual2 = c(SSD~BM,MS~BS,BM~MS,BS~Act),
  Natural = c(SSD~BM,MS~BS,BS~SSD,MS~SSD,BS~Act),
  Combined = c(SSD~BM,MS~BS,SSD~MS,BS~Act)
)
```

where Act: activity, SSD: sexual size dimorphism, BM: body size, BS: Breeding system, and MS: mating system (MS is replaced by  $I_m$  in the set of four models that used variance in genetic paternity). These functions use regression equations (or formulas) to express the hypothesized relationships in the models. The `define_model_set` function produces a set of matrices that summarize the connections between the variables. Once the model set is produced, the path analysis is performed using the `phylo_path` function. This function estimates regression using phylogenetic generalized least squares and Pagel's lambda, which measure the phylogenetic signal, i.e. the extent to which correlations in traits reflect their shared evolutionary history; When binary data are included (MS, BS, Act), `logistic_MPLE` (from the `phyloim` package) is used (van der Bijl, 2018). For each model, the program produces the following types of results (`phylopath` package in R):

- $k$  &  $q$ : are the number of conditional independencies and of parameters estimated, respectively.
- $C$ -statistic: when  $p > 0.05$  means that the model cannot be rejected.

Finally, I used `phylopath` to estimate the relative importance of each path in the best causal models by estimating the standardized path regression coefficients.

## Results

The four models of mammalian evolution (Fig. 1) were tested in two phylogenetic path analyses that used two different datasets. In one dataset, mating system measured the intensity of sexual selection, whereas in the other,  $I_m$  was used. In both analyses, the natural selection model ranked higher than the other models (Table 1): (i)  $C$  values were non-significant for the natural selection model and substantially lower than for the other models; (ii) the natural selection model received substantial support according to the  $\Delta CICc$  criterion and (iii)  $w$  yielded maximal values for the natural selection model and very low values for the other models (Table 1).

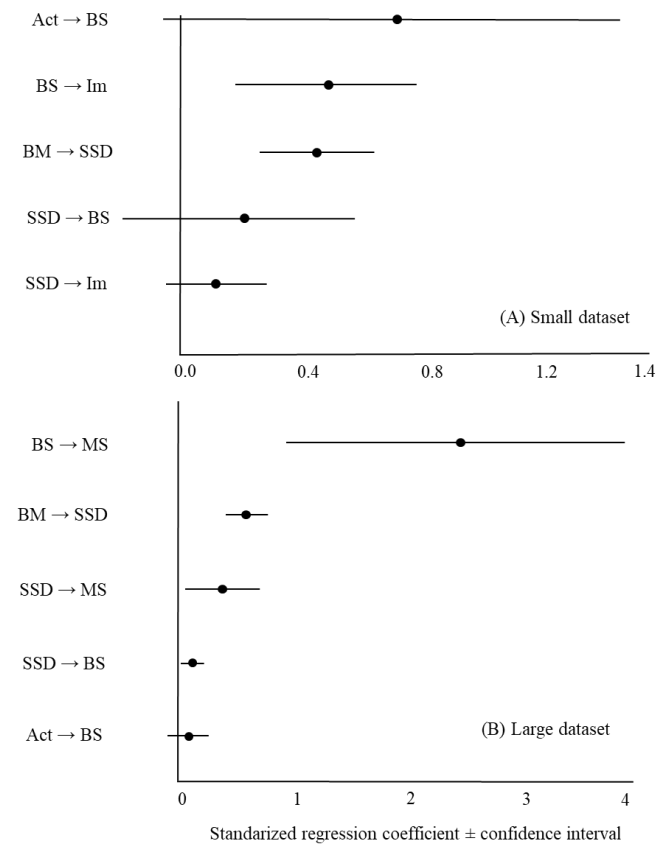
The results regarding the components of the models, i.e., the causal links between pairs of characters, were as follows (Fig. 2 and Fig. 3):

- In both analyses, the change in the breeding system led to a significant increase in the levels of polygyny ( $BS \rightarrow MS$ ) and the opportunity for sexual selection ( $BS \rightarrow I_m$ ).

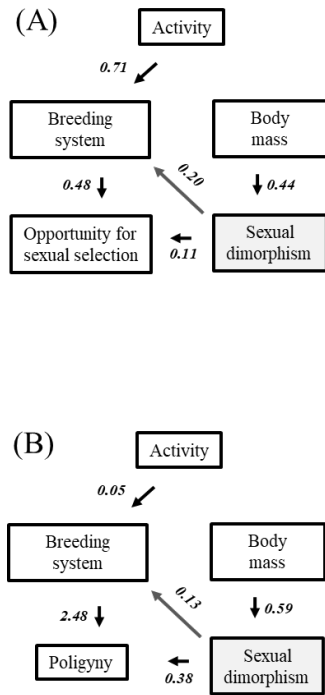
**Table 1** – Results of the phylogenetic confirmatory path analysis: Fisher's C statistic, degree of freedom *p*, C statistic information criterion C<sub>ICc</sub>, ΔC<sub>ICc</sub> (values <2 are considered to have substantial support), *w* (a measure of the strength of evidence, 0<*w*<1).

Model	k	q	C	p	C <sub>ICc</sub>	ΔC <sub>ICc</sub>	w
<i>Small dataset (I<sub>m</sub>)</i>							
Natural	5	10	10	0.437	31.8	0	0.98
Sexual2	6	9	20.5	0.058	39.9	8.13	0.02
Combined	6	9	22.3	0.034	41.7	9.92	0.0068
Sexual1	7	8	37.9	0.0005	55	23.22	0.0001
<i>Large dataset (mating system)</i>							
Natural	5	10	18.4	0.05	38.7	0	1.00
Combined	6	9	56.7	0.0001	74.9	36.2	0.0001
Sexual2	6	9	61.2	0.0001	79.4	40.7	0.0001
Sexual1	7	8	124.3	0.0001	140.5	101.8	0.0001

- In both analyses, an increase in body size implied a significant increase in sexual dimorphism (*BM* → *SSD*).
- In both analyses, an increase in sexual size dimorphism influenced group breeding (*SSD* → *BS*), but it was only statically significant when using mating system.
- In both analyses, dimorphism increased the opportunity for sexual selection (*SSD* → *I<sub>m</sub>*, non-statically significant) and the change from monogamy to polygyny (*SSD* → *MS*, statically significant).
- In any of the two analyses, sexual size dimorphism was not found to be caused by an increase in the intensity of sexual selection (*MS* → *SSD*) or (*I<sub>m</sub>* → *SSD*).



**Figure 2** – Results of the phylogenetic confirmatory path analysis for the top model (natural selection): standardized regression coefficients ± confidence interval for path components of the average of the best model. Act: daily activity, BS: breeding system, Im: intensity of sexual selection, BM: body mass, SSD: sexual size dimorphism, MS: mating system.



**Figure 3** – A visualization of the best supported causal model, with the standardized path coefficients. Using (A) opportunity of sexual selection and (B) mating system.

### Discussion

In both phylogenetic confirmatory path analyses, natural selection models performed better than sexual selection models. For the causal links between pairs of characters, path analyses suggested that (i) sexual dimorphism was causally linked to large body size (*BM* → *SSD*) and (ii) sexual dimorphism facilitated mate competition and sexual selection (*SSD* → *I<sub>m</sub>*/*MS*). In contrast, the prediction that dimorphism evolved in a polygynous context with high opportunity of sexual selection (*MS*/*I<sub>m</sub>* → *SSD*) received poor support in the path analyses.

As it was described in the Introduction, several authors have suggested that sexual dimorphism can evolve by natural selection. This evolutionary scenario was originally described by Darwin (1871) in the following words: “As the male has to search for the female, he requires for this purpose organs of sense and locomotion, but if these organs are necessary for the other purposes of life, as is generally the case, they will have developed through natural selection” (p. 168). Darwin used organs as an example, but the same reasoning can be applied to body size. Size dimorphism may have evolved “for other purposes of life”, i.e. as an ecological adaptation of males for foraging efficiency, protection against predators, or thermoregulation (Fairbairn, 1997; Slatkin, 1984; Plavcan, 2011).

Thus, the evolution of sexual size dimorphism appears to be a prerequisite for the evolution of polygyny. A larger body size could have been also advantageous for obtaining mates, promoting the evolution of this mating system. While large males could take advantage of their larger size to obtain more mates, smaller males would develop alternative tactics, such as sperm competition. As a result, males compete for females using different mating strategies that depend on body size (Kokko and Jennions, 2008) and are maintained in the populations by equilibrium sexual selection (Cassini, 2020).

In the introduction, it was described that ancestral mammals were supposed to be nocturnal, monomorphic, solitary and with low levels of polygyny and intensity of sexual selection. Most extant mammalian taxa retain these characteristics (Ralls, 1977). The mammalian orders with high levels of polygyny and sexual size dimorphism are artiodactyls, pinnipeds, and primates (Ralls, 1977). Previous studies described the processes that would have triggered these evolutionary changes in each of these three taxa. Krüger et al., 2014 applied this path analysis to 11 life-history traits in 35 pinniped species to infer the most likely

evolutionary trajectories in the evolution of this taxon. They found that sexual size dimorphism evolved prior to changes in the mating system. They suggested that a shift toward deeper dives, related to changes in water temperature, would have selected for larger size in males, enabling niche partitioning between the sexes. In primates, the model that received the most support from path analyses was a mixed model in which dimorphism evolved after an increase in body size that resulted from a response to a change from nocturnal to diurnal habits, with the consequent increase in the risk of predation (Shultz et al., 2011; Cassini, 2023). In artiodactyls, path analysis indicated that the trigger for the evolutionary pathway toward an increase in body size, gregariousness, and dietary specialization was a shift from close to open habitat (Jarman, 1974). Sexual size dimorphism appeared to evolve mostly after niche separation between males and females (Cassini, 2022a). In summary, phylogenetic path analyses of the evolution of sexual size dimorphism conducted in pinnipeds, primates and artiodactyls separately, suggested that natural selection may have an important role in the evolution of sexual size dimorphism.

The traditional way of investigating the evolution of sexual dimorphism in mammals consisted of comparative studies that showed positive correlations between dimorphism and different behavioural measures of sexual selection intensity, the most common being the pattern of spatial distribution of males and females during the reproductive period and species mating systems. This approach has been used in artiodactyls (Clutton-Brock et al., 1980; Loison et al., 1999; Pérez-Barbería et al., 2002; Bro-Jorgensen, 2007), primates (Lindenfors and Tullbert, 1998; Jones et al., 2009), and pinnipeds (Boness, 1991; Lindenfors et al., 2002). Positive correlations between sexual size dimorphism and reproductive group size or levels of polygyny were interpreted as evidence that that reproductive competition promoted the evolution of large males, the causal link  $I_m/MS \rightarrow SSD$  in the path analyses. The problem is that correlations do not explain causation and, therefore, the opposite causal relationship ( $SSD \rightarrow I_m/MS$ ) can also explain these correlations.

Confirmatory path analysis is a relatively new tool used in phylogenetic studies that allows researchers to evaluate and compare causal models using observational data (van der Bijl, 2018). As just described the results obtained in this and other recent studies that applied path analysis tend to revalue the role of natural selection in the evolution of sexual dimorphism in mammals and, therefore, do not always coincide with those obtained with traditional methods, which supports the hypothesis that intra-male precopulatory directional sexual selection is the most important selective force. Another important methodological change in sexual selection studies was the way of estimating its intensity. Traditionally, different behavioural measures were used, such as breeding group size, mating systems, or operational sex ratios (Mitani et al., 1996; Clutton-Brock et al., 1977, 1980; Lindenfors and Tullbert, 1998; Loison et al., 1999). Currently, it is recognized that the best measure of sexual selection intensity is paternity analysis of offspring using molecular techniques because it rules out the possibility that apparently nonmating males are nevertheless successful in extra-group copulations (Wade and Shuster, 2004). In mammals, several studies showed the discrepancies between behavioral and genetic measures of fitness; furthermore, the introduction of molecular markers is demonstrating that extra-group fertilization is widespread among mammals, with the consequence of a decrease in male reproductive skew, thus the intensity of sexual selection (Coltman et al., 1999; Young and Bennett, 2013; Isvaran and Sankaran, 2017; Cassini, 2022a).

The most accepted theory regarding the evolution of dimorphism states the intra-male precopulatory directional sexual selection as the most important selective force (Alexander et al., 1979; Hedrick and Temeles, 1989; Shine, 1989; Loison et al., 1999; Isaac, 2005; Dubuc et al., 2014).

New studies using modern statistical and genetic tools are required to establish the proper causal evolutionary paths in mammalian evolution. ☞

## References

Akaike H., 1974. A new look at the statistical model identification, IEEE Transactions on Automatic Control 19(6): 716–723. doi:10.1109/TAC.1974.1100705

- Alexander R.M.N., Jayes A.S., Maloiy G.M.O., Wathuta E.M., 1979. Allometry of limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). J. Zool. Lond. 189: 305–314.
- Andersson M., 1994. Sexual selection (Vol. 72). Princeton University Press.
- Arnold S.J., Wade M.J., 1984. On the measurement of natural and sexual selection: theory. Evolution 709–719.
- Baker J., Meade A., Pagel M., Venditti C., 2015. Adaptive evolution toward larger size in mammals. Proceedings of the National Academy of Sciences 112(16): 5093–5098.
- Bonnes D.J., 1991. Determinants of mating systems in the Otariidae (Pinnipedia). In: Renouf D. (Ed.) The Behaviour of Pinnipeds. Chapman & Hall, New York, USA. 1–44.
- Bro-Jorgensen J., 2007. The intensity of sexual selection predicts weapon size in male bovids. Evolution 61: 1316–1326.
- Burnham K.P., Anderson D.R., Huyvaert K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral ecology and sociobiology 65(1): 23–35.
- Burnham K.P., Anderson D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2<sup>nd</sup> ed. Springer, Berlin.
- Cardon M., Loot G., Grenouillet G., Blanchet S., 2011. Host characteristics and environmental factors differentially drive the burden and pathogenicity of an ectoparasite: a multilevel causal analysis. J. Anim. Ecol. 80: 657–667.
- Cassini M.H., 1999. The evolution of reproductive systems in pinnipeds. Behavioral Ecology 10(5): 612–616.
- Cassini M.H., 2020. A mixed model of the evolution of polygyny and sexual size dimorphism in mammals. Mammal Review 50(1): 112–120.
- Cassini M.H., 2021. Sexual aggression in mammals. Mammal Review, 51(2): 247–255.
- Cassini M.H., 2022. Evolution of sexual size dimorphism and sexual segregation in artiodactyls: the chicken or the egg? Mammalian Biology 102(1): 131–141.
- Cassini M.H., 2023. Role of sexual and natural selection in the evolution of sexual size dimorphism in primates. Journal of Zoology 320(1): 53–62.
- 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. Molecular Ecology 8(7): 1199–1209.
- Clutton-Brock T.H., 1988. Reproductive success. Chicago, IL: University of Chicago Press. 472–486.
- Clutton-Brock T.H., Albon S.D., Harvey H., 1980. Antlers, body size and breeding group size in the Cervidae. Nature 285: 565–566.
- Clutton-Brock T.H., Harvey P.H., Rudder B., 1977. Sexual dimorphism, socioeconomic sex ratio and body weight in primates. Nature 269(5631): 797–800.
- Cranford T.W., 1999. The sperm whale's nose: sexual selection on a grand scale? Marine mammal science 15(4): 1133–1157.
- Darwin C., 1871. The Descent of Man, and Selection in Relation to Sex. John, London, UK.
- Dines J.P., Mesnick S.L., Ralls K., May-Collado L., Agnarsson I., Dean M.D., 2015. A trade-off between precopulatory and postcopulatory trait investment in male cetaceans. Evolution 69(6): 1560–1572.
- Dubuc C., Ruiz-Lambides A., Widdig A., 2014. Variance in male lifetime reproductive success and estimation of the degree of polygyny in a primate. Behavioral Ecology 25(4): 878–889.
- Emlen S.T., Oring L.W., 1977. Ecology, sexual selection and the evolution of mating systems. Science 197: 215–223.
- Fairbairn D.J., 1997. Allometry for sexual size dimorphism: pattern and process in the co-evolution of body size in males and females. Annual Review of Ecology and Systematics 28: 659–682.
- Gonzalez-Voyer A., von Hardenberg A., 2014. An introduction to phylogenetic path analysis. In: Garamszegi L.Z. (Ed.) Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology. Springer-Verlag, Berlin, Heidelberg. 201–229.
- Gordon A.D., 2006. Scaling of size and dimorphism in primates II: microevolution. International Journal of Primatology 27: 63–105.
- Hagen B.L., Kumschick S., 2018. The relevance of using various scoring schemes revealed by an impact assessment of feral mammals. NeoBiota 38: 37–75.
- Hedrick A.V., Temeles E.J., 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. Trends in Ecology and Evolution 4: 136–138.
- Isaac J.L., 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. Mammal Review 35: 101–115.
- Isvaran K., Sankaran S., 2017. Do extra-group fertilizations increase the potential for sexual selection in male mammals? Biology Letters 13: 283–295.
- Janis C.M. 1982. Evolution of horns in ungulates: ecology and paleoecology. Biol. Rev. Camb. Philos. Soc 57: 261–317.
- Jarman P., 1974. The social organisation of antelope in relation to their ecology. Behaviour 48: 215–267.
- Jones K.E., Bielby J., Cardillo M., Fritz S.A., O'Dell J., Orme C.D.L., Safi K., Sechrest W., Boakes E.H., Carbone C., Connolly C., Cutts M.J., Foster J.K., Grenyer R., Habib M., Plaster C.A., Price S.A., Rigby E.A., Rist J., Teacher A., Bininda-Emonds O.R.P., Gittleman J.L., Mace G.M., Purvis A., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90: 2648.
- Kokko H., Jennions M.D., 2008. Parental investment, sexual selection and sex ratios. Journal of Evolutionary Biology 21(4): 919–948.
- Krüger O., Wolf J.B.H., Jonker R.M., Hoffman J.L., Trillmich R., 2014. Disentangling the contribution of sexual selection and ecology to the evolution of size dimorphism in pinnipeds. Evolution 68: 1485–1496.
- Le Boeuf B.J., 1974. Male-male competition and reproductive success in elephant seals. American Zoologist 14: 163e176.
- Le Boeuf B.J., Crocker D.E., Costa D.P., Blackwell S.B., Webb P.M., Houser D.S., 2000. Foraging ecology of northern elephant seals. Ecological Monographs 70: 353e382
- Leutenegger W., Cheverud J., 1985. Sexual dimorphism in Primates. The effects of size. In: Jungers W.L. (Ed.) Size and Scaling in Primate Biology. Plenum, New York. 33–60.
- Lindenfors P., 2002. Sexually antagonistic selection on primate size. Journal of Evolutionary Biology 15(4): 595–607.
- Lindenfors P., Gittleman J.L., Jones K.E., 2007. Sexual size dimorphism in mammals. In: Fairbairn D.J., Blanckenhorn W.U., Székely T. (Eds.) Sex, size, and gender roles: Evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford. 16–26.

- Lindenfors P., Tullberg B.S., Biuw M., 2002. Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology* 52: 188–193.
- Lindenfors P., Tullberg B.S., 1998. Phylogenetic analyses of primate size evolution: the consequences of sexual selection. *Biological Journal of the Linnean Society* 64: 413–447.
- Loison A., Gaillard J.-M., Pelabon C., Yoccoz N.G., 1999. What factors shape sexual size dimorphism in ungulates? *Evol. Ecol. Res.* 1: 611–633
- Lukas D., Clutton-Brock T.H., 2013. The evolution of social monogamy in mammals. *Science* 341(6145): 526–530.
- Lukas D., Clutton-Brock T., 2020. Monotony and the evolution of plural breeding in mammals. *Behavioral Ecology* 31(4): 943–949.
- Maor R., Dayan T., Ferguson-Gow H., Jones K.E., 2017. Temporal niche expansion in mammals from a nocturnal ancestor after dinosaur extinction. *Nature ecology & evolution* 1(12): 1889–1895.
- Mitani J.C., Gros-Louis J., Richards A.F., 1996. Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *Am. Nat.* 147(6): 966–980.
- Pérez-Barbería F.J., Gordon I.J., 2000. Differences in body mass and oral morphology between the sexes in the Artiodactyla: Evolutionary relationships with sexual segregation. *Evol. Ecol. Res.* 2: 667–684.
- Pérez-Barbería F.J., Gordon I.J., Pagel M., 2002. The origins of sexual dimorphism in body size in ungulates. *Evolution* 56(6): 1276–1285.
- Plavcan J.M., 2001. Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology* 44: 25–53.
- Plavcan J.M., 2011. Understanding dimorphism as a function of changes in male and female traits. *Evolutionary Anthropology* 20: 143–155.
- Plavcan J.M., 2004. Sexual selection, measures of sexual selection, and sexual dimorphism in primates. *Sexual selection in primates*, 230.
- Ralls K., 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *The American Naturalist*, 111(981): 917–938.
- Rensch B., 1950. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. *Bonner Zoologische Beiträge* 1: 58–69. [in German]
- Schulte-Hostedde A.I., 2007. Sexual size dimorphism in rodents. *Rodent societies: An ecological and evolutionary perspective* 115(128): 5.
- Shine R., 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *The Quarterly Review of Biology* 64: 419–461.
- Shipley B., 2000. *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge Univ. Press, Cambridge, U.K.
- Shipley B., 2013. The AIC model selection method applied to path analytic models compared using ad-separation test. *Ecology* 94(3): 560–564.
- Shultz S., Opie C., Atkinson Q.D., 2011. Stepwise evolution of stable sociality in primates. *Nature* 479: 219–222.
- Silva M., 1998. Allometric scaling of body length: Elastic or geometric similarity in mammalian design. *Journal of Mammalogy* 1: 20–32.
- Slatkin M., 1984. Ecological causes of sexual dimorphism. *Evolution* 38: 622–630
- Smith R.J., 1999. Statistics of sexual size dimorphism. *Journal of Human Evolution* 36(4): 423–458.
- Stulp G., Barrett L., 2016. Evolutionary perspectives on human height variation. *Biological Reviews* 91(1): 206–234.
- Trillmich F., Trillmich K.G.K., 1984. The mating systems of pinnipeds and marine iguanas: convergent evolution of polygyny. *Biological Journal of the Linnean Society* 21: 209–216.
- van der Bijl W., 2018. *phylopath: easy phylogenetic path analysis in R*. PeerJ 6: e4718.
- von Hardenberg A., Gonzalez-Voyer A., 2012. Disentangling evolutionary cause-effect relationships with phylogenetic confirmatory path analysis. *Evolution* 67(2): 378–387.
- Wade M., Shuster S.M., 2004. Sexual selection: harem size and the variance in male reproductive success. *The American Naturalist* 164(4): E83–E89.
- Weckerly F.W., 1998. Sexual-size dimorphism: Influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* 79: 33–52.
- Wrangham R.W., 1980. An ecological model of female-bonded primate groups. *Behaviour* 75(3–4): 262–300.
- Young A.J., Bennett N.C., 2013. Intra-sexual selection in cooperative mammals and birds: why are females not bigger and better armed? *Philos Trans. R. Soc. Lond. B Biol. Sci.* 368: 20130075.

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## Supplemental information

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

**Supplement S1** Dataset.

**Supplement S2** Consensus phylogenetic tree.

**Supplement S3** List of additional references.