

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.

Keywords: body size, path analysis, mating system, genetic paternity

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 (Fairbain, 1977). Dimorphism in other features, such as teeth, horns, pelage or brain size, is typically a consequence of size dimorphism (Pérez-Barbería & 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 & Barrett, 2016).

Sexual size dimorphism may have evolved through two processes: sexual or natural selection (Darwin, 1871; Slatkin, 1984; Pavlan, 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; Pavlan, 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 distances and thus reach the best but most distant foraging areas (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 & 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 & 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 & Oring,1977; Lukas & 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; Fairbain, 1997; Weckerly, 1998).

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 & 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 & 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 (Figure 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 (Figure 1a; Boness, 1991; Lindenfors & 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 (Figure 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 (Clutton-Brock

et al., 1984; Andersson, 1994; Fairbairn, 1997; Lindenfors et al., 2007; Lindenfors et al., 2002; Gordon, 2006).

Another model proposed that sexual size dimorphism evolved through natural selection (Figure 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 & 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 & Trillmich, 1984; Cassini, 2021), which in turn favoured the evolution of plural breeding females (Emlen & Oring, 1979; 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 & Wade, 1984; Kokko & Jennions, 2008; Isvaran & 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 (Figure 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 (Hardenberg & 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 reproduction (Gonzalez-Voyer & 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 & von Hardenberg, 2014).

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 & Gordon, 2000), primates (Gordon, 2006), cetaceans (Dines et al., 2015), and rodents (Schulte-Hostedde, 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 Supplementary Information). 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 & 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., Lindenfors, 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 $I_m = var/mean^2$ (Arnold & 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 (Supplementary Information). 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 & 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 (Supplementary information). 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 (2020), 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 (Figure 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 (Hardenberg & Gonzalez-Voyer, 2012). In structural equation models, causal relationships are translated into a set of linear equations that follow a causal structure (Gonzalez-Voyer & Hardenberg, 2014). Shipley (2000a) 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 & Hardenberg, 2014).

Shipley (2000b) then proposed combining the p -values using Fisher's C statistic, which is calculated as $C = -2 \sum_{i=1}^k (\ln(p_i))$, where k is the number of conditional independencies in the minimum set and p is their p -value. The C statistic follows a χ^2 distribution, with $df = 2k$, thereby providing a method for determining the goodness of fit of the entire path model (Gonzalez-Voyer & 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 Hardenberg and Gonzalez-Voyer (2014) proposed a criterion similar to Akaike's

information criterion (Akaike, 1974) called the C statistic information criterion, which is calculated as $CICc = C + 2q \times \frac{n}{(n-1-q)}$, 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 & 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 (2018), 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). 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 Supplementary material). I incorporated four models (represented graphically in Figure 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 *Im* 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 *phylolm* 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 (Figure 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 (Figure 2 and 3):

1. 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 ($BS \rightarrow I_m$).
2. In both analyses, an increase in body size implied a significant increase in sexual dimorphism ($BM \rightarrow SSD$).
3. In both analyses, an increase in sexual size dimorphism influenced group breeding ($SSD \rightarrow BS$), but it was only statically significant when using mating system.
4. In both analyses, dimorphism increased the opportunity for sexual selection ($SSD \rightarrow I_m$, non-statically significant) and the change from monogamy to polygyny ($SSD \rightarrow MS$, statically significant).
5. In any of the two analyses, sexual size dimorphism was not found to be caused by an increase in the intensity of sexual selection ($MS \rightarrow SSD$) or ($I_m \rightarrow SSD$).

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 ($BM \rightarrow SSD$) and (ii) sexual dimorphism facilitated mate competition and sexual selection ($SSD \rightarrow I_m/MS$). In contrast, the prediction that dimorphism evolved in a polygynous context with high opportunity of sexual selection ($MS/I_m \rightarrow SSD$) 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 (Fairban, 1977; 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 & 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, 2022). 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 & 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 ($SSD \rightarrow Im/MS$) 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 & Tullberg, 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 & 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 (Coltamn et al., 1999; Young & Bennett, 2013; Isvaran & Sankaran, 2017; Cassini, 2022).

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 & 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.

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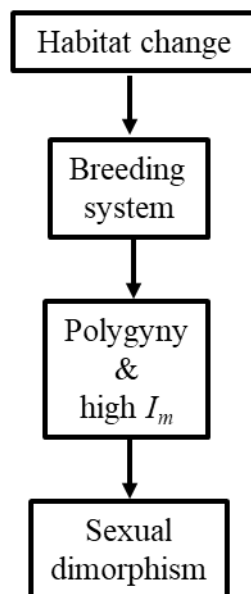
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Table 1. Results of the phylogenetic confirmatory path analysis: Fisher's C statistic, degree of freedom p, C statistic information criterion CICc, Δ CICc (values < 2 are considered to have substantial support), w (a measure of the strength of evidence, $0 < w < 1$).

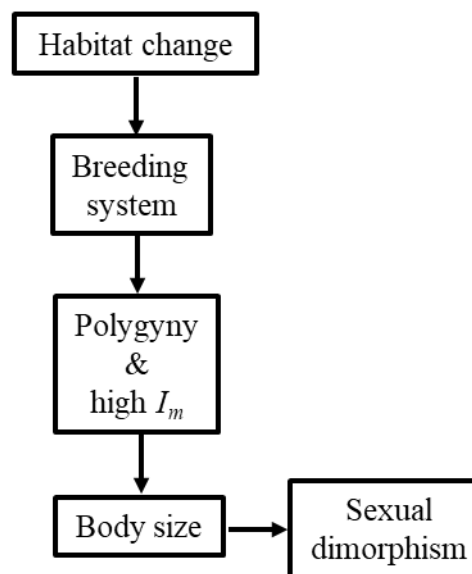
Model	k	q	C	p	CICc	Δ CICc	w
<i>Small dataset (I_m)</i>							
Natural	5	10	10	0.437	31.8	0	0.98
Sexual2	6	9	20.5	0.058	39.9	8.13	0.02
Combined	6	9	22.3	0.034	41.7	9.92	0.0068
Sexual1	7	8	37.9	0.0005	55	23.22	0.0001
<i>Large dataset (mating system)</i>							
Natural	5	10	18.4	0.05	38.7	0	1.00
Combined	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

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

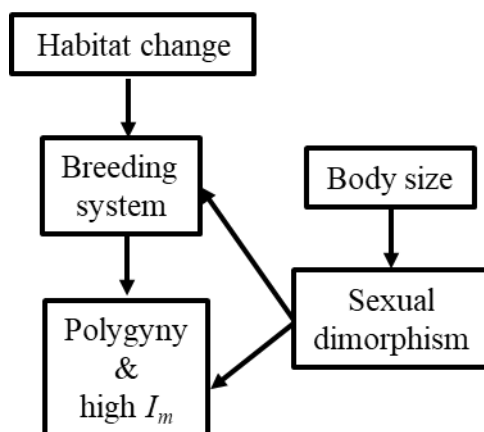
(A) Sexual selection model



(B) Sexual selection model v.2



(C) Natural selection model



(D) Combined model

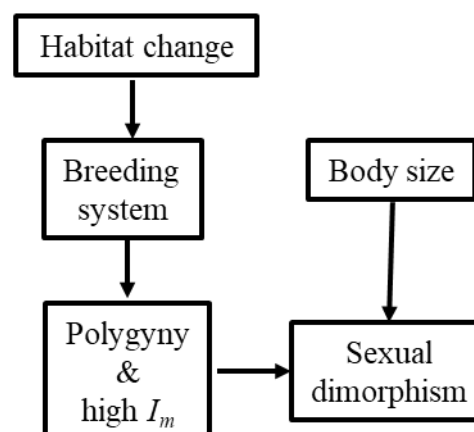


Figure 2. Results of the phylogenetic confirmatory path analysis for the top model (natural selection): standardized regression coefficients \pm confidence intervals for path components of the average of the best model. Act: daily activity, BS: breeding system, Im: intensity of sexual selection, BM: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

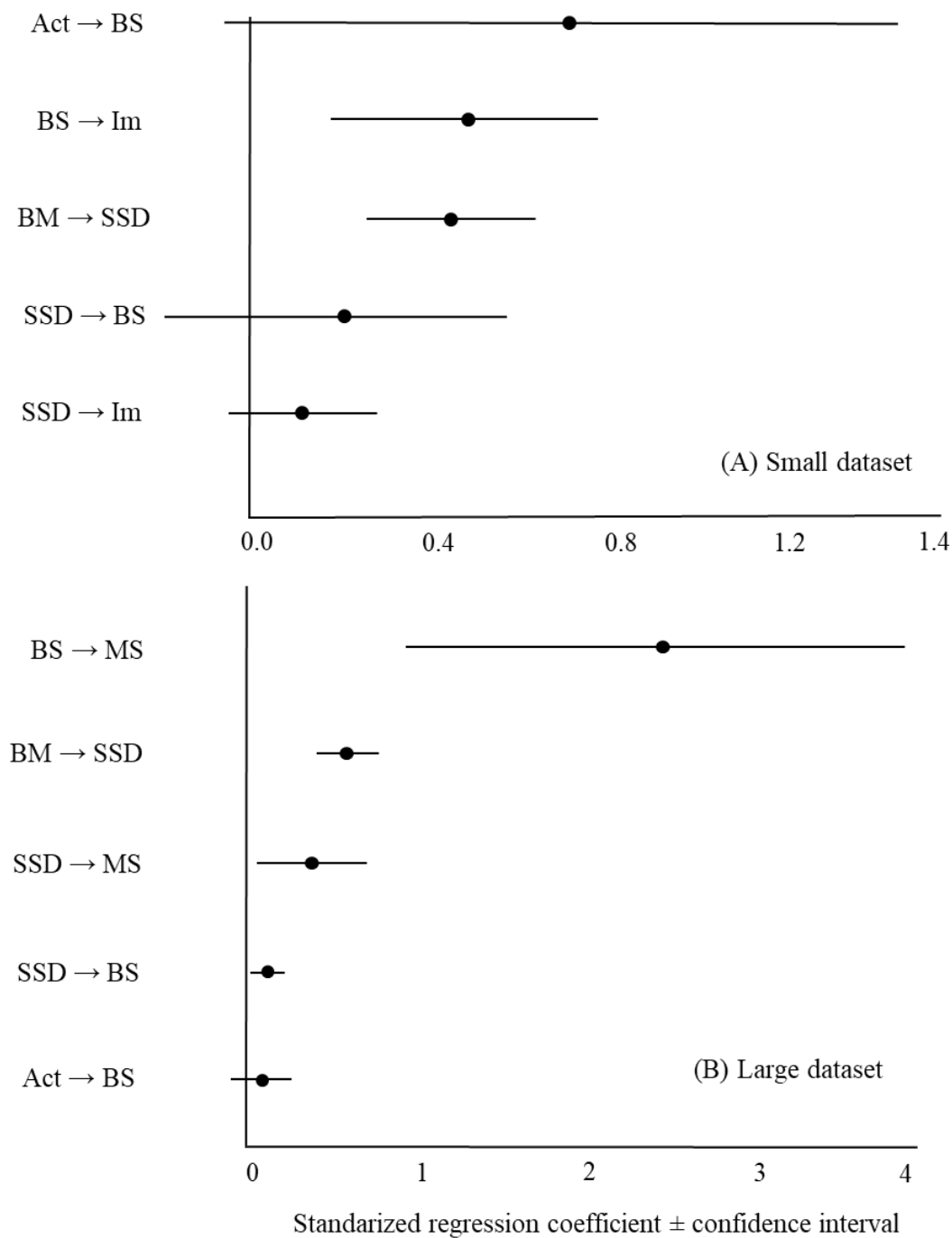
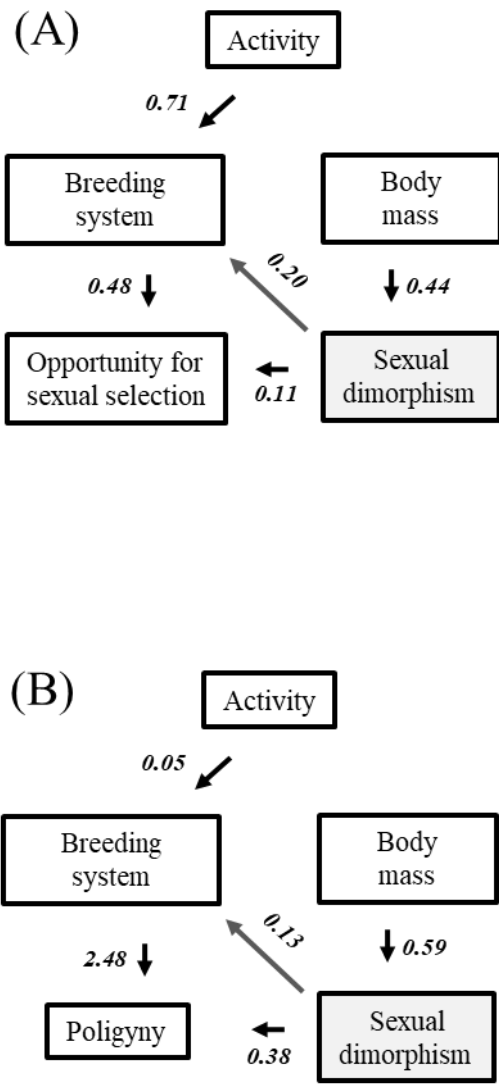


Figure 3. A visualization of the best supported causal model, with the standardized path coefficients. Using (A) opportunity of sexual selection and (B) mating system



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