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SHORT COMMUNICATION

Sexual dimorphism in toothed whales (Odontoceti) follows Rensch's rule

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Abstract

Rensch's rule entails that male-biased sexual size dimorphism scales allometrically with body size and is assumed to generally apply to polygynous taxa. However, so far only few mammalian groups have been shown to conform to it. Toothed whales (Odontoceti) not only span a substantial range of body sizes, but are commonly presumed to be predominantly polygynous, thus representing a promising candidate group to test for Rensch's rule. Here we compiled a dataset of sex-specific body lengths in 57 species of toothed whales and demonstrate that sexual size dimorphism in this group does indeed follow Rensch's rule. When focusing on selected subgroups of toothed whales, conformity to the rule was prominent among lineages of the speciose superfamily Delphinoidea, while it was not found in the beaked whales of the family Ziphiidae. These results support the assumption that polygynous and polygynandrous mating systems and marked precopulatory intrasexual competition between males are common among toothed whales. However, female-biased sexual size dimorphism as well as monomorphism occur at notable frequencies as well, suggesting that reproductive strategies are nevertheless variable among these marine mammals.

Keywords Sexual selection · Intrasexual competition · Marine mammals · Body size scaling

Rensch's rule proposes that among closely related species, sexual size dimorphism (SSD) scales allometrically with body size (Abouheif and Fairbairn 1997). It assumes that relative SSD increases with body size when males are the larger sex (male-biased SSD; Rensch 1950) and vice versa when the opposite is the case (female-biased SSD; Rensch 1960, but see Webb and Freckleton 2007). One important evolutionary driver behind this pattern is assumed to be sexual selection, particularly due to intrasexual competition between males (reviewed in Lindenfors et al. 2007; see also Dale et al. 2007). In line with this, Rensch's rule appears restricted to polygynandrous and polygynous taxa among vertebrates and is not found in monogamous ones or among polyandrous species (Dale et al. 2007, but see Caspar et al. 2021). Indeed, the rule has been found to be sex-reversed in some polyandrous groups (Dale et al. 2007).

In mammals polygyny and polygynandry are the predominant mating systems (Mesnick and Ralls 2008). However, although Rensch's rule appears to hold for mammals as a group (Lindenfors et al. 2007), few studies so far found SSD scaling in compliance with it on lower taxonomic levels such as orders or families (Lindenfors et al. 2007; Martinez et al. 2014; Wu et al. 2018). Hence, the rule's general applicability to mammalian taxa, even those that are strongly polygynous, remains uncertain and requires further investigation. Toothed whales (Odontoceti) and particularly their most speciose taxon, the Delphinoidea (oceanic dolphins, porpoises, narwhals, and beluga whales), represent an interesting model group to study the phenomenon because they encompass a substantial range of body sizes while likely exhibiting polygynous or polygynandrous mating systems throughout, which are typically characterized by high intrasexual competition between males (Mesnick and Ralls 2008). This condition is expected to favor the evolution of male-biased SSD and conformity to Rensch's rule (Dale et al. 2007; Lindenfors et al. 2007). However, so far, such mating systems have

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only been effectively confirmed in just a few model species (Dines et al. 2015).

In most toothed whales, sexually dimorphic body size is indeed apparent and male-biased, while females are usually the larger sex in baleen whales (see Ralls and Mesnick 2009 for discussion of underlying factors). Female-biased SSD has mostly been reported for the smallest toothed whales, including river dolphins (Kasuya 1972; Anli and Kayia 1992; except *Inia*—Martin and Da Silva 2006) and the diminutive oceanic dolphins of the genus *Cephalorhynchus* (Heimlich-Boran 1993), but it also occurs in beaked whales (Omura et al. 1955). Besides often being significantly larger than the opposite sex, males in diverse odontocete species also display various sexual ornaments. These include enlarged and/or conspicuously formed fins and flippers as well as post-anal humps in dolphins and porpoises (Ralls and Mesnick 2009), modified dentition in beaked whales and the narwhal (Silverman and Dunbar 1980; Heyning 1984; Dines et al. 2015), and dimorphic skull size and shape in sperm whales and beaked whales (Nakamura et al. 2013; Gol'din 2014). Males in more dimorphic species tend to exhibit smaller testes relative to their body size, which indicates that their reproductive success is strongly dependent on precopulatory measures, including physical competition (Dines et al. 2015; but see MacLeod 2010). In line with this, male odontocetes typically show higher levels of intrasexual aggression than females, which can result in extensive sex-specific scarring (Silverman and Dunbar 1980; Heyning 1984; MacLeod 1998; Martin and Da Silva 2006; Lee et al. 2019). Apart from killer whales (*Orcinus orca*) and several globicephaline dolphins, associations between adult male and female odontocetes are weak and largely restricted to the context of mating (May-Collado et al. 2007; Möller 2012).

Earlier studies have shown that larger-bodied species of oceanic dolphins (Delphinidae) tend to show markedly greater sexual dimorphism than smaller ones (Heimlich-Boran 1993; Möller 2012) but previous analyses did not address the phylogenetic interdependence of species data and it has never been tested whether these differences follow an allometric scaling compliant with Rensch's rule. A study on body mass SSD in ten non-identified cetacean species recovered no compliance to the rule, (Lindenfors et al. 2007) but the small size and undisclosed composition of the sample calls for further investigation.

We assembled a dataset of adult sex-specific body lengths in 57 odontocete species from all extant families to approximate the expression and scaling of SSD in these aquatic mammals. All collected data with notes on sample sizes and geographic provenance of sampled populations are included in Table S1. We chose body length rather than body mass as a size proxy, since both are highly correlated (Heimlich-Boran 1993) but little data is available on the latter for many odontocetes. Mean body lengths for males and females were used to calculate SSD ratios (see Table S1), following the method of Smith (1999), which were rounded to the second decimal [m/f if SSD is male biased, SSD values > 1; 2-(f/m) if it is female biased, SSD values < 1; an SSD value of 1 indicates monomorphism]. For a species to be included, data for at least three adult individuals of each sex were required. If no other datasets were available, the mean body length for each sex was derived from studies presenting sex-specific growth models of the species in question (e.g., Plön 2004). The asymptotic values for body length were then assumed to represent the mean body length of the respective sex (annotated in Table S1). When we encountered markedly different SSD values in distinct populations of a species (e.g., Northern vs. Southern hemisphere populations, killer whale types, etc.), we adopted the most extreme one.

To test whether Rensch's rule applies to toothed whales as a whole as well as to their three most speciose subgroups (Delphinidae, Monodontidae + Phocoenidae clade, Ziphiidae) we employed phylogenetic reduced major axis (pRMA) regression, which is a well-established method to investigate SSD scaling (Abouheif and Fairbairn 1997; Caspar et al. 2021). The phylogenetic relationships between the taxa analyzed need to be statistically addressed because shared ancestry results in non-independence of species-specific data points. We performed pRMA regressions of $\log_{10}$ (male body length) on $\log_{10}$ (female body length) by aid of the *phytools* package in R (*phyl.RMA* function*;* Revell 2012). In taxa where male-biased SSD is predominant, such as odontocetes, Rensch's rule is considered to hold when the regression coefficient β is significantly greater than 1, indicating hyperallometric scaling (Abouheif and Fairbairn 1997). SSD scaling conforming to $\beta = 1$ (isometry) or $\beta < 1$ (hypoallometry) would refute it. Deviation of β from an isometric scaling pattern was assessed with Clarke's T statistic with adjusted degrees of freedom. Pagel's λ was employed to measure the phylogenetic signal in the data.

Our nomenclature follows the Society of Marine Mammalogy's committee on taxonomy (2021) (except for the application of the revised nomenclature for dolphins formerly grouped under *Lagenorhynchus* by Vollmer et al. 2019). We adopted the phylogeny and branch lengths for the analyses from McGowen et al. (2009). One species, the Australian snub-fin dolphin (*Orcaella heinsohni*) was not included in that study and was instead manually added to our tree using the divergence dating from Vilstrup et al. (2011). Note that molecular studies recovered a number of commonly recognized delphinid genera (and also *Phocoena*) to be non-monophyletic, explaining their scrambled appearance in the tree (Perrin et al. 2013).

We found that the majority of odontocetes (60%, $n_{\text{species}} = 34$) display male-biased SSD (Fig. 1, Table S1). The most extreme male-biased SSD is expressed in the sperm whale (*Physeter macrocephalus*; SSD ratio: 1.52),

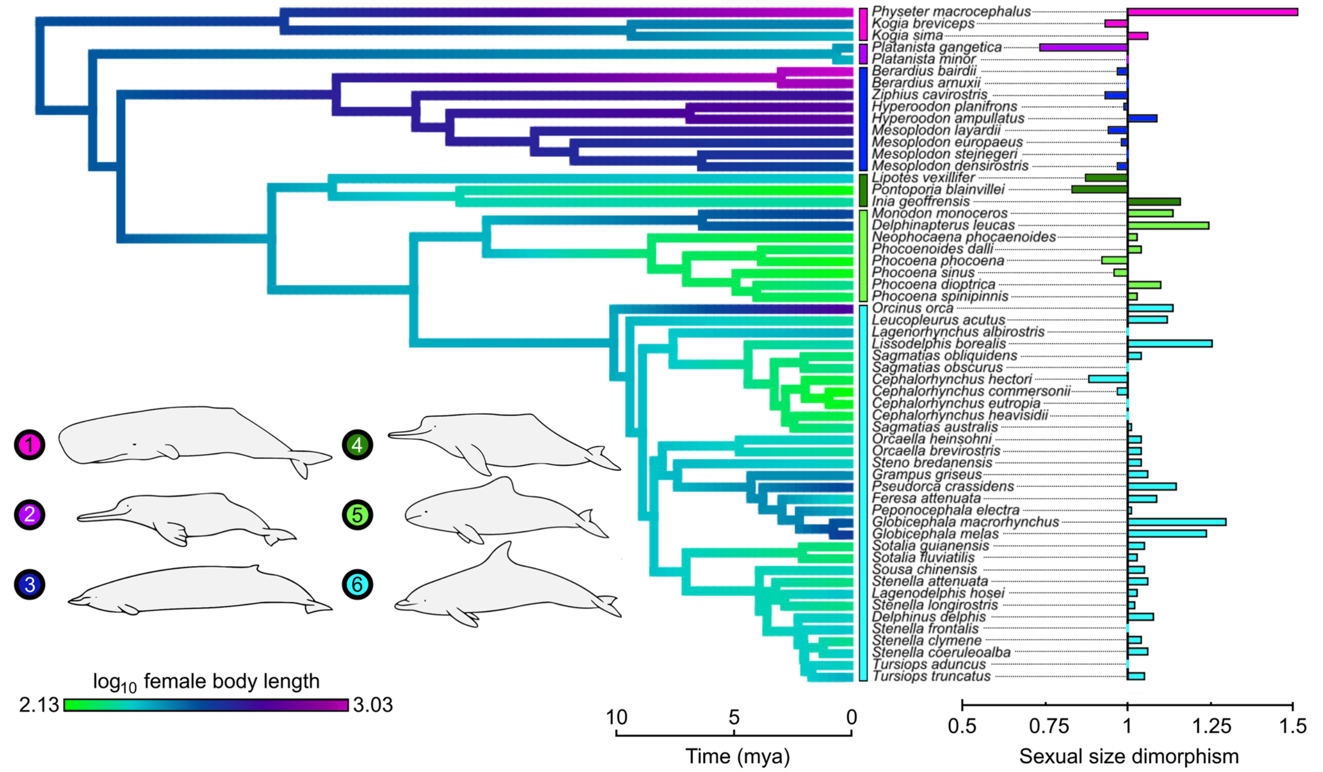

Fig. 1 Phylogenetic distribution of sexual body length dimorphism in odontocetes. The color-coding of the tree corresponds to species' female body length and denotes maximum-likelihood estimates for ancestral female body size at each node [plotted with the *contMap()* function of the *phytools* package]. The bar plot visualizes sexual size dimorphism: <1 = female-biased, 1 = monomorphic (no bar), >1 = male-biased. Clades are color-coded in the bar plot: 1 Physeteroidea, 2 Platanistidae, 3 Ziphiidae, 4 Inoidea, 5 Monodontidae & Phocoenidae, 6 Delphinidae. Line art by Chris Huh (CC BY-SA 3.0), not to scale

short-finned pilot whale (*Globicephala macrorhynchus*; 1.3), Northern right whale dolphin (*Lissodelphis borealis*; 1.26), and beluga whale (*Delphinapterus leucas*; 1.25). Female-biased SSD (26%, $n_{\text{species}} = 15$) was frequent among beaked whales, small-bodied delphinoids and the two clades of river dolphins. The Ganges river dolphin (*Platanista gangetica*) was the most dimorphic species with female-biased SSD (0.72), followed by the franciscana (*Pontoporia blainvillei*; 0.83) and the baiji (*Lipotes vexillifer*; 0.87). Sexually monomorphic species were rare (14%, $n_{\text{species}} = 8$) but found across major groups. Examples include the Atlantic spotted dolphin (*Stenella frontalis*), Indus River dolphin (*Platanista minor*), and Arnoux' beaked whale (*Berardius arnuxii*).

The pRMA regression models revealed Rensch's rule to hold for toothed whales as a whole, as indicated by significant hyperallometric SSD scaling (Fig. 2a; $\beta = 1.175$, $p < 0.0001$). It was also evident among the Delphinidae (Fig. 2b; $\beta = 1.172$, $p = 0.002$) and the clade formed by the families Monodontidae and Phocoenidae (Fig. 2c; $\beta = 1.273$, $p = 0.005$). In beaked whales, Rensch's rule was not recovered and SSD scaling followed an isometric trajectory (Fig. 2d; $\beta = 1.045$, $p = 0.551$). SSD entailed a strong phylogenetic signal (Pagel's $\lambda \geq 0.9$) in all groups analyzed (Fig. 2). However, this estimate can only be considered robust for odontocetes as a whole and for delphinids, given that the species samples for the remaining two clades were small (Freckleton et al. 2002).

Our results demonstrate the validity of Rensch's rule in odontocetes, which is consistent with the assumption of widespread polygyny and polygynandry combined with significant physical male–male competition (Dale et al. 2007) in this group (Mesnick and Ralls 2008). Still, female-biased SSD as well as monomorphism were recovered surprisingly often occurring in 40% of the studied species. Conforming to Rensch's rule, female-biased SSD and monomorphism was mostly found in small-bodied species (the ziphiids represent an exception to this trend and will be discussed below), while species with body lengths exceeding 2.5 m typically displayed varying degrees of male-biased SSD. The latter pattern could in parts relate to female reproductive demands. While small cetaceans experience natural selection pressures restricting their body size (Galatius 2010), females will benefit from maintaining a certain body mass to successfully deliver and nurse calves (Ralls 1976; Slooten 1991). Indeed, relative to their body size, small odontocetes give birth to the largest neonates among cetaceans (a pattern

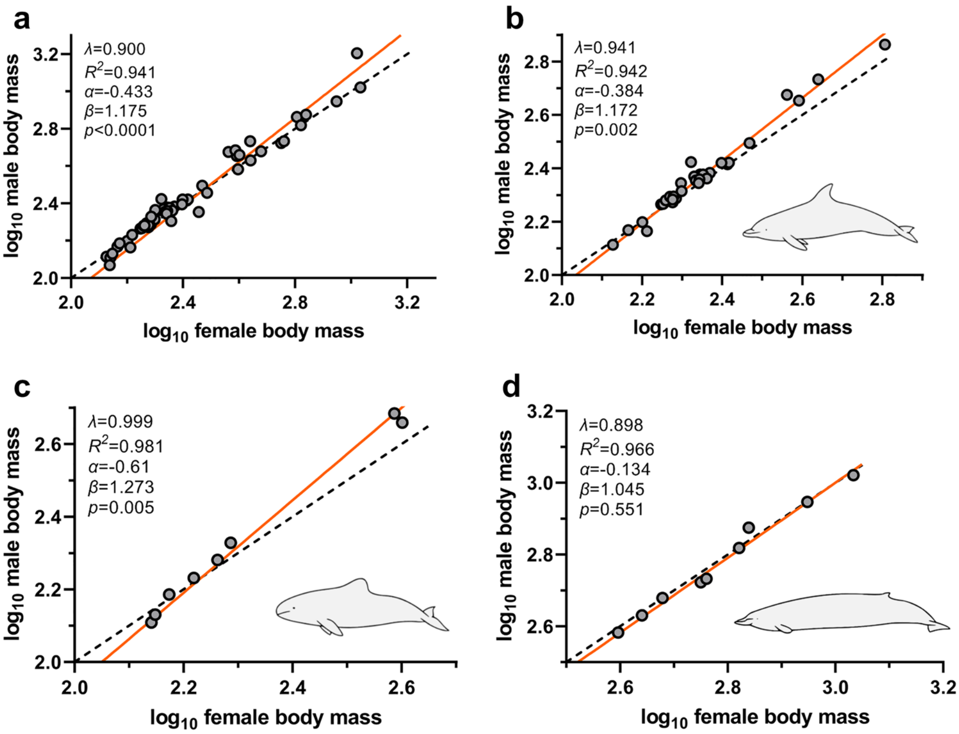

Fig. 2 Scaling of sexual size dimorphism in toothed whales (Odontoceti) as recovered by phylogenetic major reduced axis models. Broken lines indicate a size ratio of 1.0 between the sexes, equating to isometric scaling. Orange lines correspond to the regression coefficient β, which indicates the actual trajectory of scaling. Rensch's rule is indicated here by a significant deviation of $\beta > 1$ ($\beta = 1$ corresponds to sexual monomorphism), which is realized in odontocetes in general (**a**; $n = 57$), Delphinidae (**b**; $n = 32$), and the Monodontidae-Phocoenidae clade (**c**; $n = 8$), but not in the Ziphiidae (**d**; $n = 9$). Pagel's λ: phylogenetic signal [can vary from 0 (absent) to 1 (very strong)], R^2: coefficient of determination, α: intercept, β: regression coefficient. p values indicate the probability of $\beta = 1$. Line art by Chris Huh (CC BY-SA 3.0), not to scale

also observed in other mammalian orders, see Martin and MacLarnon 1985), providing a particular challenge to the mother (Ohsumi 1966). At the same time, males in such small-bodied species tend to show adaptations to sperm competition instead of physical combat (Van Waerebeek and Read 1994; Fontaine and Barette 1997). Different from many monomorphic terrestrial mammals, there is no evidence for monogamous mating strategies in monomorphic or weakly dimorphic cetaceans. The only species, for which there is notable data in support of a monogamous mating system is the franciscana (Wells et al. 2013), in which SSD is strongly female-biased (Fig. 1).

In species with male-biased SSD, which are mostly represented by medium to large-sized delphinoids and the sperm whale, it can be expected that sexual conflicts are more likely to be decided through precopulatory measures than in ones with different SSD patterns. Such measures might include ritualized but potentially violent confrontations in which greater body size would be advantageous. However, reports on aggressive intrasexual competition are rare in wild cetaceans (Parsons et al. 2003). Due to the limitations of surface observations, such events are often simply inferred from bite and rake marks (Heimlich-Boran 1993), the visibility and persistence of which varies considerably between species (MacLeod 1998). However, raking is a comparatively mild agonistic action that not only occurs in aggressive but also in play contexts (Grimes et al. 2022). During more intense fights, several odontocete species engage in ramming and tail slapping. These behaviors can severely damage inner organs but do not leave visible cutaneous lesions (Gowans and Rendell 1999; Parsons et al. 2003; Oremland et al. 2010; Robeck et al. 2019). The frequency and threat imposed by such behaviors might therefore easily be underestimated, complicating assessments of their effects in a given species (Robeck et al. 2019). Hence, the extent to which aggressive behaviors are employed in intrasexual competition in odontocetes remains unclear but their significance could be substantial. In any case, the conformity to Rensch's rule as well as other available evidence is consistent with the idea that such conflicts play a role in male reproductive behavior across several major odontocete lineages (Ralls and Mesnick 2009). Interestingly, pronounced male-biased SSD is found in several philopatric delphinid species that form modular multi-male/multi-female groups organized around matrilines, such as pilot whales and killer whales (see Heimlich-Boran 1993). At least for the latter, it was suggested that male reproductive success correlates positively with body size (eastern North Pacific residents—Ford et al. 2011). How different social systems interplay with body size to determine SSD in toothed whales remains a multifaceted issue to unravel.

Despite their comparatively large size, beaked whales appear to consistently display female-biased SSD or sexual monomorphism. The only exception to this pattern that we found is the Northern bottlenose whale (*Hyperoodon ampullatus*), but note that several beaked whales, particularly the genera *Indopacetus* and *Tasmacetus*, were not sampled here due to the extreme scarcity of available biometric data. Beaked whales represent the only one of the three speciose subgroups of odontocetes studied herein that does not follow Rensch's rule. The absence of male-biased SSD among these cetaceans has long been noted (Omura et al. 1955) but is surprising because males in many species display notably small testes and elaborate sex-specific weapons that are evidently used against same-sex conspecifics (Heyning, 1984; Dines et al. 2015; but see MacLeod 2010 on the potential importance for sperm competition in some beaked whales). More research on these understudied marine mammals is required to explain this counterintuitive trait combination. In any case, the contrasting patterns of SSD expression suggest that reproductive competition in beaked whales differs markedly from that in most delphinoid cetaceans. The same might well be true for some of the river dolphins (compare Wells et al. 2013; but note that intense male–male aggression and male-biased SSD is characteristic for *Inia*—Martin and Da Silva 2006) and the dwarf sperm whale (*Kogia sima*) that also lack male-biased SSD patterns and that all appear to live either solitarily or in small, non-cohesive groups (May-Collado et al. 2007). Unfortunately, the reproductive biology of many of these species is only poorly understood.

Finally, an important limitation of this study needs to be pointed out: our dataset provides only an incomplete picture of SSD patterns among the toothed whales because it does not consider intraspecific variation. Indeed, regional differences in SSD and reproductive strategies within single species can be pronounced (Perrin and Mesnick 2003; Ferguson et al. 2021) and understanding their causes could help to make sense of general SSD variation within and between odontocete groups. Future research might focus on whether Rensch's rule also holds when intraspecific SSD patterns in toothed whales are considered and should address how reproductive strategies differ between taxa that conform to it, such as oceanic dolphins, compared to those that do not, like the beaked whales.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42991-022-00239-1.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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