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A trade-off between precopulatory and postcopulatory trait investment in male cetaceans

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Mating with multiple partners is common across species, and understanding how individual males secure fertilization in the face of competition remains a fundamental goal of evolutionary biology. Game theory stipulates that males have a fixed budget for reproduction that can lead to a trade-off between investment in precopulatory traits such as body size, armaments, and ornaments, and postcopulatory traits such as testis size and spermatogenic efficiency. Recent theoretical and empirical studies have shown that if males can monopolize access to multiple females, they will invest disproportionately in precopulatory traits and less in postcopulatory traits. Using phylogenetically controlled comparative methods, we demonstrate that across 58 cetacean species with the most prominent sexual dimorphism in size, shape, teeth, tusks, and singing invest significantly less in relative testes mass. In support of theoretical predictions, these species tend to show evidence of male contests, suggesting there is opportunity for winners to monopolize access to multiple females. Our approach provides a robust dataset with which to make predictions about male mating strategies for the many cetacean species for which adequate behavioral observations do not exist.

KEY WORDS: Morphological evolution, reproductive strategies, sexual selection, trade-offs.

Sexual selection is a potent evolutionary force shaping morphological diversity within and among species (Darwin 1871; Eberhard 1985; Andersson 1994; Birkhead and Møller 1998; Eberhard 2009). In the framework of game theory, individual males have a fixed energy budget from which to invest in traits that are adaptive in precopulatory and/or postcopulatory arenas of reproduction (Parker 1998; Parker and Pizzari 2010; Parker et al. 2013). Understanding how males allocate their resources to reproduction remains a fundamental objective in evolutionary biology.

Postcopulatory competition occurs when a female mates with multiple males and their sperm compete for access to her ova (Parker 1970). One prediction of sperm competition theory is that as its intensity increases, males are predicted to invest more in spermatogenesis to win paternity (Parker 1990, 1998). Consistent with this prediction, testes mass (relative to body mass) is positively correlated with the intensity of sperm competition across

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a diversity of taxa (Harcourt et al. 1981; Kenagy and Trombulak 1986; Møller 1989; Stockley and Purvis 1993; Gage 1994; Stockley et al. 1997; Hosken and Ward 2001; Pitcher et al. 2005; Ramm et al. 2005; Firman and Simmons 2008; Simmons and García-González 2008), although not all of these studies controlled for potential phylogenetic effects. Even within species, males from populations with relatively high sperm competition invest in larger testes (Firman and Simmons 2008), as do males that adopt "sneaker" mating strategies that result in higher levels of sperm competition (Stockley and Purvis 1993; Gage et al. 1995; Stockley et al. 1997; Taborsky 1998; Simmons et al. 1999; Neff et al. 2003; Schulte-Hostedde et al. 2005; Rudolfsen et al. 2006; Simmons et al. 2007; Montgomerie and Fitzpatrick 2009; Simmons and Fitzpatrick 2012). Experimental evolution studies confirm that males exposed to intense sperm competition invest more in testes (Hosken and Ward 2001; Pitnick et al. 2001; Yamane et al. 2010). Testes investment has also been associated with the manufacture of competitively superior sperm (Stockley et al. 1997; Simmons et al. 1999; Vladić and Järvi 2001; Anderson and Dixson 2002; Burness et al. 2004; Snook 2005; Fitzpatrick et al. 2007; Locatello et al. 2007; Lüpold 2013; Young et al. 2013), proportionately more seminiferous tubules (Harcourt et al. 1981; Lüpold et al. 2009; Firman et al. 2015) and increased rates of spermatogenesis (Parapanov et al. 2008; Gómez Montoto et al. 2012).

Although they are presumably adaptive under strong sperm competition, large testes and increased spermatogenesis come at a cost. Relatively unfit individuals are less able to sustain testes mass and rates of spermatogenesis (Olsson et al. 1997; Schulte-Hostedde et al. 2005) and spermatogenesis reduces life span in some animals (Van Voorhies 1992). Importantly, male mate choice implies that ejaculates are costly to produce and conserved when possible (Dewsbury 1982; Wedell et al. 2002; Drickamer et al. 2003; Ramm and Stockley 2014).

Given the costs, investment in testes is expected to trade-off against investment in precopulatory traits, and this has been demonstrated within species. *Onthophagus* beetles that were experimentally prevented from developing horns developed larger relative testes (Simmons and Emlen 2006). Conversely, experimental ablation of the precursor cells of genitalia in *Onthophagus* resulted in exaggerated growth of horns (Moczek and Nijhout 2004). In some systems, there is a positive correlation between investment in precopulatory and postcopulatory phenotypes (Kelley et al. 2014), which could occur if overall resource acquisition increases (Devigili et al. 2013).

In contrast to studies within species, the trade-off between pre- and postcopulatory traits across a phylogeny is only predicted for species where males can monopolize access to multiple females (Parker et al. 2013; Lüpold et al. 2014). For such species, males are expected to invest disproportionately in precopulatory

phenotypes such as weaponry because the potential payoff is large. These males reduce investment in postcopulatory phenotypes such as testis size because all available energy has been invested in precopulatory phenotypes and/or because sperm competition is so rare that investment in spermatogenesis has reduced payoff. This form of male–male competition is known as contest competition because selection favors males that win contests.

In species where males cannot monopolize access to multiple females, selection favors males that locate and inseminate females using both pre- and postcopulatory traits, a strategy known as scramble competition. In contrast to contest competition, scramble competition is expected to lead to a positive correlation between pre- and postcopulatory traits, contrary to the trade-off hypothesis (Malo et al. 2005; Locatello et al. 2006; Rogers et al. 2008; Lüpold et al. 2014). Because the ability of a male to monopolize access to multiple females decreases as the number of estrous females increases, the expected relationship between precopulatory and postcopulatory phenotypes may vary depending on mating opportunities (Preston et al. 2003). Consistent with these theoretical predictions (Parker et al. 2013), Lüpold et al. (2014) found that correlations between pre- and postcopulatory investment range from positive (no trade-off) for species engaging in scramble competition to negative (trade-off) for species engaging in contest competition.

Perhaps due to the complications of interspecific comparisons, very few studies have detected the theoretical trade-off between pre- and postcopulatory traits across a phylogeny. In a study of 72 mammalian species, Gage et al. (2002) found no evidence for a trade-off between precopulatory (sexual size dimorphism [SSD]) and postcopulatory (relative testes mass) traits. Across 58 artiodactyls, Ferrandiz-Rovira et al. (2014) found no evidence of a trade-off between weapon size and testes mass. In contrast, Fitzpatrick et al. (2012) documented a trade-off between precopulatory (SSD) and postcopulatory (relative testes mass as well as baculum length) traits in 14 species of pinnipeds. Interestingly, the relationship in the latter study was driven by harem-forming species, where males engage in contest competition to monopolize access to multiple females. In an analysis of 112 species of parasitic worms, there was a trade-off between pre- and postcopulatory traits (Poulin and Morand 2000), and a large proportion of species appear to monopolize access to multiple females (Lüpold et al. 2014).

Cetaceans offer a unique perspective on the trade-off hypothesis. Females are highly mobile and reside in groups of varying sizes and social composition, which can be clustered or dispersed over large geographic ranges. The mating season can be condensed or prolonged, females may ovulate once or multiple times and interbirth intervals can range from one to over five years, all of which can affect operational sex ratio (Boness et al. 2002). It is thus not surprising that the basic mating strategy of male cetaceans

appears to be searching for receptive females and spending little time with them other than to mate (Mesnick and Ralls 2002). However, males of some species employ mate guarding long enough to increase assurance of paternity (Wells et al. 1987; Connor et al. 1996; Willis and Dill 2007) or form longer term bonds (Wells et al. 2013).

Here, our primary goal is to test for a trade-off between precopulatory and postcopulatory traits across the cetacean phylogeny, and to place our results in the context of cetacean mating behavior. Our study provides insight into the factors driving evolutionary trade-offs between male precopulatory and postcopulatory investment in this enigmatic group.

Materials and Methods

All analyses were performed using the statistical package R (www.r-project.org). The script to run various analyses below is supplied as in File S1.

ESTIMATING THE STRENGTH OF POSTCOPULATORY SEXUAL SELECTION

We estimated investment in postcopulatory sexual selection using phylogenetically controlled residuals of maximum testes mass regressed onto maximum body length. From the literature, we gathered maximum body length and maximum combined testes mass for 58 of the 90 currently recognized species of cetaceans (Committee_on_Taxonomy 2014; Table S1). Some of these data were previously compiled as part of studies on sperm competition in baleen whales (Brownell and Ralls 1986), cetacean mating systems (Mesnick and Ralls 2002), sexual dimorphism (Ralls and Mesnick 2002; Perrin and Mesnick 2003), and pelvic bone evolution (Dines et al. 2014). When possible, we report the maximum weight of both testes, without the epididymides, from healthy, mature males collected during the mating season, using histological examination or field observations of sperm in the epididymides to confirm sexual maturity. Testes masses reported in the literature sometimes included epididymides, sometimes did not, and sometimes did not specify. When testes included epididymides, it was rarely possible to apply a known correction for the weight and we retained the combined weight in the analysis. Unknown inclusion or exclusion of epididymides should only add noise to our analyses, making our conclusions conservative. In studies where the mass of a single testis was reported, we doubled the value, consistent with the documented similarity in left and right testis weights in many cetacean species (Lockyer 1986).

We focused on maximum reported testes mass because testes regress outside of the breeding season, and different populations within the same species can show divergence in breeding season (Perrin and Reilly 1984). Testes weights taken from beached an-imals may be underestimates of their weight in life, however we do not expect a systematic bias in testing predictions of trade-off theory; all species should be equally affected. All data appear in Table S1. We used maximum body length in the analyses rather than maximum body mass because weighing cetaceans, especially the larger species, is rarely done, and using weights from beached animals may lead to underestimates because the animal may have been malnourished before beaching or because the specimen may have degraded prior to examination.

ESTIMATING THE STRENGTH OF PRECOPULATORY SEXUAL SELECTION

The strength of precopulatory sexual selection is often estimated using the proxy of SSD, with the idea that selection favors larger size in males that engage in contests (Darwin 1871; Trivers 1972; Clutton-Brock and Harvey 1977; Clutton-Brock et al. 1977; Lindenfors et al. 2007). For all species for which we had testes size data, we also collected morphological data from the literature (Table S1), then estimated the intensity of precopulatory sexual selection with two different approaches. First, SSD was calculated as the log (maximum reported body length of sexually mature males/maximum reported body length of sexually mature females; Table S1) and used as a quantitative proxy for the intensity of precopulatory sexual selection.

Second, we compared species that possess prominent precopulatory phenotypes to those that do not. We focused on traits that likely influence the outcomes of male–male contest competition through aggressive interactions, such as weapons and large body size. We also included dimorphic traits such as enlarged dorsal fins and song that could influence the outcomes of male–male contests through dominance displays. Of the 58 species in our dataset, there were 17 species that possessed one or more exaggerated male traits, including extreme sexual size or shape dimorphism, the presence of dimorphic dentition (battle teeth or tusks), and/or male-specific song (Fig. 1).

Outliers in size dimorphism were identified by plotting two measures: (1) (observed SSD minus phylogenetic mean SSD)/phylogenetically controlled standard deviation versus (2) observed SSD minus SSD predicted from conditional multivariate probability (File S1). These two measures were highly correlated (Fig. S1). Species that were outliers in SSD included the sperm whale (*Physeter macrocephalus*, Fig. 1A), whose males can be up to 63% longer than females, nearly four times as heavy, and possess a greatly enlarged head and spermaceti organ and make unique male-specific sounds (Rice 1989); pilot whales (genus *Globicephala*), the males of which are more than 30% larger than females, have larger and more bulbous heads, larger and thicker dorsal fins, and deeper tail stocks (Jefferson et al. 2008); and the northern right whale dolphin (*Lissodelphis borealis*), in which males are more than 30% longer than females (Table S1, Fig. S1).
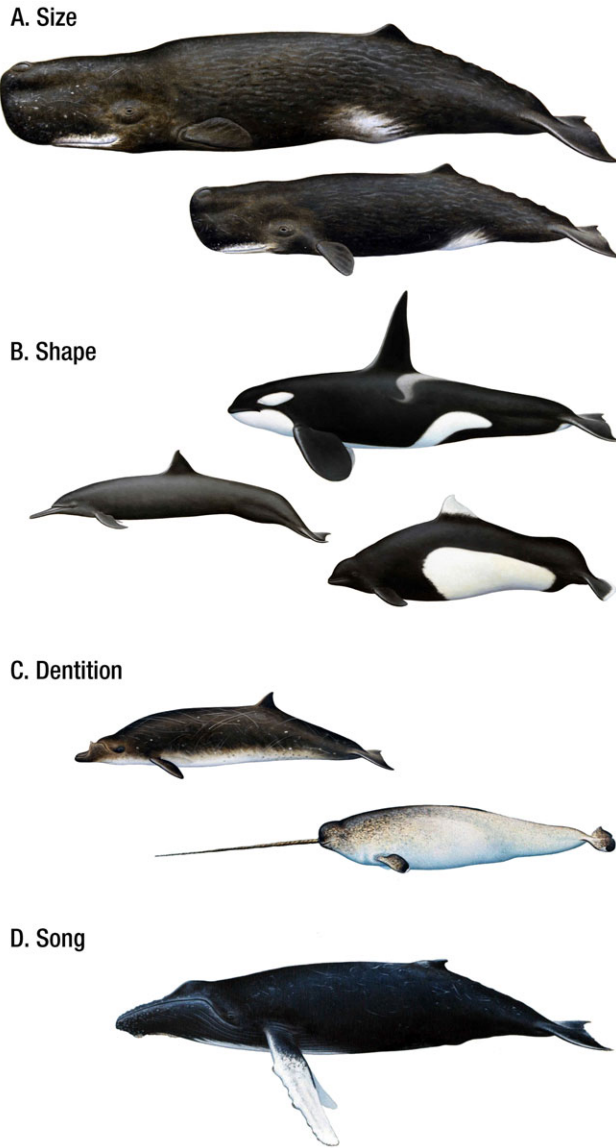
Figure 1. Examples of "prominent" precopulatory traits. Artwork by Brett Jarrett and graphics by Su Kim; images not drawn to scale. (A) Extreme sexual size dimorphism seen in the sperm whale (*Physeter macrocephalus*, male above, female below). (B) Extreme shape dimorphism seen in male killer whale (*Orcinus orca*, top), eastern spinner dolphin (*Stenella longirostris orientalis*, middle), and Dall's porpoise (*Phocoenoides dalli*, bottom). Females not shown. (C) Sexually dimorphic teeth. "Battle teeth" and sex-specific scarring of Blainville's beaked whale (*Mesoplodon densirostris*, top) and tusks of narwhal (*Monodon monoceros*, bottom). (D) Male song in the humpback whale (*Megaptera novaeangliae*).

Species with strong sexual shape dimorphism included Dall's porpoise (*Phocoenoides dalli*; Fig. 1B), the eastern spinner dolphin (*Stenella longirostris orientalis*; Fig. 1B), and killer whales (*Orcinus orca*; Fig. 1B). Dall's porpoise and eastern spinner dolphin males are slightly larger than females, and also have forward-

canted dorsal fins, enlarged postanal humps and differently shaped flukes than their female conspecifics (Jefferson 1990; Perrin 1990; Perrin et al. 1991; Perrin 1998). Male Dall's porpoise also have enlarged thoracic epaxial muscles and deepened caudal peduncles which may confer strength and maneuverability in agonistic interactions (Jefferson 1990). Females lack these features. Although the degree of dimorphism varies among numerous forms of killer whales, males typically have longer body length, larger body mass, greater girth, greatly enlarged and erect dorsal fins, and their flippers are larger and shaped differently than females (Dahlheim and Heyning 1999).

Species with sexually dimorphic dentition (Fig. 1C) included the narwhal (*Monodon monocerus*; Fig. 1C) in which males possess a greatly elongated tooth that can grow up to 2.7 m (Best 1981), and several species of beaked whales. In the beaked whale genus *Mesoplodon*, a single pair of mandibular teeth erupts only in mature males. The teeth project up and outside the mouth and are apparently used for intraspecific fighting with other males for access to females (Heyning 1984; Mead 1989a; Pitman 2008). The teeth vary in size, position, degree of eruption, presence of a sharp denticle at the top, and are sometimes raised on a bony arch of the lower jaw (Mead 1989a; Jefferson et al. 2008). This variation may correlate with differing amounts of male aggression among the different species (Pitman 2008). Many of these species also have secondary ossification of the mesorostral canal, thought to strengthen the rostrum during fights (Heyning 1984; Mead 1989a; de Buffrenil and Casinos 1995; MacLeod 2002).

Additional beaked whale species that have sexually dimorphic dentition include Cuvier's beaked whale (*Ziphius cavirostris*), which also has a densely ossified rostrum (Heyning 1989), and the bottlenose whale (*Hyperoodon ampullatus*), whose single pair of teeth erupt only in mature males but are nearly obscured by their greatly enlarged and flattened foreheads composed of massive bony crests on the maxillary bones which are thought to be used in headbutting contests between adult males (Mead 1989b; Gowans et al. 2001).

Due to the variation in tooth morphology, not all beaked whale species were considered to be prominently sexually dimorphic (Heyning 1984; Mead 1989a; Dalebout et al. 2008). Specifically, two species, True's beaked whale (*Mesoplodon mirus*) and Shepherd's beaked whale (*Tasmacetus shepherdi*), were not included in the prominent precopulatory group despite having sexually dimorphic dentition. The small pair of apical teeth in *M. mirus* is inconspicuous and barely extends past the gums. In *T. shepherdi*, males have an extra pair of small conical teeth at the tip of the jaw, but both males and females possess a full set of teeth and males lack mesorostral reinforcement (Mead 1989a).

Male song represents a behavioral precopulatory trait that may mediate social interactions and affect access to potential mates (Payne and McVay 1971; Darling 2009; Herman et al.

2013). Much remains to be learned about the function of song, but species in which only males sing include the humpback whale (*Megaptera novaeangliae*, Fig. 1D), blue whale (*Balaenoptera musculus*), and fin whale (*Balaenoptera physalus*).

It is possible that evolutionary forces other than contest competition can influence all of the traits discussed above. For example, prominent precopulatory traits could be influenced by female choice or by natural selection (Selander 1966; Ralls 1976; Götmark et al. 1997; Stuart–Fox and Ord 2004; Bell and Zamudio 2012). We are unable to eliminate such alternative explanations but they should only contribute noise to our analyses, making our conclusions conservative.

ESTIMATING THE OPPORTUNITY FOR MALES TO MONOPOLIZE ACCESS TO FEMALES VIA CONTEST COMPETITION

Theory predicts that a trade-off between precopulatory and postcopulatory investment should only exist in species where males can monopolize access to multiple females (Parker et al. 2013; Lüpold et al. 2014). Unfortunately, data on cetacean mating systems are limited, so we inferred the potential for monopolization from several sources. Genetic data, when available, enabled direct estimates of the potential that males were able to monopolize access to multiple females. Such studies have shown, for example, possible increased paternity among dominant humpback males (Nielsen et al. 2001; Cerchio et al. 2005) and among male alliances in Indian Ocean bottlenose dolphins (Wiszniewski et al. 2011). Rare behavioral observations of North Atlantic right whale females simultaneously copulating with two males suggest males are unable to monopolize access to females (Mate et al. 2005). In the spinner dolphins, data on the proportion of males actively undergoing spermatogenesis suggest a few sexually and socially dominant males might control mating opportunities (Perrin and Mesnick 2003).

Much more commonly, we had to rely on indirect evidence to assess the likelihood that males could monopolize access to females. Behavioral observations of male combat and sex-specific scarring indicative of past battles suggest that males attempt to establish dominance. Other types of male–male interactions, such as tusking in male narwhals and song in humpbacks, may play a role in the establishment of a dominance hierarchy or other as yet unknown aspects of male competition (Best 1981; Darling 2009; Heide-Jørgensen 2009).

When genetic, behavioral, or life-history data were not available, we assessed the likelihood of male attempts to monopolize access to females based on the distribution of females during the breeding season, group size, and social structure, with the general idea that monopolization is not likely when females are solitary or widely dispersed during the breeding season or part of large, mixed sex groups (Table S2, Connor et al. 1998; Boness

et al. 2002; Gowans et al. 2007; May-Collado et al. 2007; Moeller 2012). In bats and rodents, for example, sperm competition is more common in large groups (Hosken 1997; Dean et al. 2006), therefore monopolization is less likely, although this pattern was not observed in bovids (Bro-Jørgensen 2007).

All our inferences regarding the likelihood that males are able to monopolize access to females via male contests are presented in Table S2. We used a "conservative" classification that included only those species for which we had genetic or behavioral information and a "relaxed" classification in which we also included indirect inferences of monopolization based on life history, female distribution, and group size (columns 3 and 4, respectively, Table S2). Our literature survey may have underestimated contest frequency or intensity if they occur out of the range of observers, if they leave no physical marks, or if they do not involve direct physical contact, for example, through acoustic rather or visual displays.

ANALYSES

Using the cetacean phylogeny and branch lengths of McGowen et al. (2009), we calculated the residuals of maximum testes mass regressed onto maximum male body length using phylogenetic generalized least squares (PGLS) implemented via the GLS procedure in the R package NLME. A correlation structure that accounted for phylogenetic relatedness (Pagel 1999) was introduced using the CORPAGEL function in the R package APE (Paradis et al. 2004). This correlation structure corrects for the expected similarity in trait values based on species relationships, while estimating lambda, the degree of phylogenetic patterning in the data.

We tested for a negative correlation between residual testes mass and SSD using PGLS incorporating the entire cetacean phylogeny (pruned for the species present in our dataset). We also tested whether the 17 species with prominent precopulatory phenotypes (Fig. 1, Table S1) had significantly smaller residual testes compared to the other species, using a phylogenetically controlled ANCOVA implemented in the PHYLANOVA function of the R package PHYTOOLS (Garland et al. 1993; Revell 2012). Significance was determined with 10,000 simulations of Brownian trait evolution on the phylogeny; the empirical *P*-value was halved to produce a one-tailed *P*-value because we tested the one-tailed hypothesis that species with prominent precopulatory phenotypes had relatively small testes.

Lastly, using BayesTraitv2 (Pagel 1994) we compared two maximum likelihood models to test whether prominent precopulatory phenotypes were more likely to evolve in concert with the potential for males to monopolize access to females. The (null) independent model estimates the $0 \rightarrow 1$ and $1 \rightarrow 0$ transition rate parameters for the two traits (four parameters total). The transition probabilities in each trait do not depend on transitions in the other state. Under the (alternative) dependent model, transitions in one
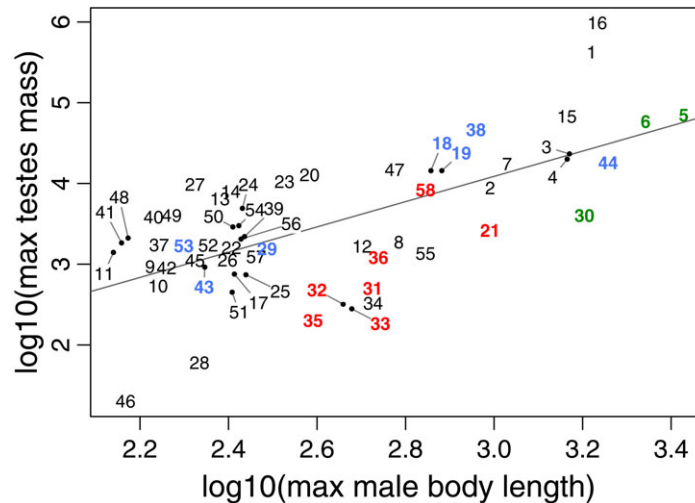
Figure 2. Relative testes mass among cetaceans. Maximum recorded combined testes mass plotted against maximum recorded body length. Solid line indicates the best fit line from an uncorrected regression. Numbers indicate the 58 cetacean species compiled for this study (see below). For clarity some are shifted from their original positions (connected by small lines). Species with prominent precopulatory traits are color-coded (blue = sexual size and/or shape dimorphism, red = sexually dimorphic dentition, green = male-specific singing, black = lack of prominent postcopulatory traits). 1—*Balaena mysticetus* (bowhead whale); 2—*Balaenoptera acutorostrata* (minke whale); 3—*Balaenoptera borealis* (Sei whale); 4—*Balaenoptera edeni* (Bryde's whale); 5—*Balaenoptera musculus* (blue whale); 6—*Balaenoptera physalus* (fin whale); 7—*Berardius bairdii* (Baird's beaked whale); 8—*Caperea marginata* (pygmy right whale); 9—*Cephalorhynchus commersonii* (Commerson's dolphin); 10—*Cephalorhynchus heavisidii* (Heaviside's dolphin); 11—*Cephalorhynchus hectori* (Hector's dolphin); 12—*Delphinapterus leucas* (beluga whale); 13—*Delphinus capensis* (long-beaked common dolphin); 14—*Delphinus delphis* (short-beaked common dolphin); 15—*Eschrichtius robustus* (gray whale); 16—*Eubalaena japonica* (North Pacific right whale); 17—*Feresa attenuata* (pygmy killer whale); 18—*Globicephala macrorhynchus* (short-finned pilot -whale); 19—*Globicephala melas* (long-finned pilot whale); 20—*Grampus griseus* (Risso's dolphin); 21—*Hyperoodon ampullatus* (bottlenose whale); 22—*Inia geoffrensis* (boto); 23—*Kogia breviceps* (pygmy sperm whale); 24—*Kogia sima* (dwarf sperm whale); 25—*Lagenorhynchus acutus* (Atlantic white-sided dolphin); 26—*Lagenorhynchus obliquidens* (Pacific white-sided dolphin); 27—*Lagenorhynchus obscurus* (dusky dolphin); 28—*Lipotes vexillifer* (baiji); 29—*Lissodelphis borealis* (Northern right whale dolphin); 30—*Megaptera novaeangliae* (humpback whale); 31—*Mesoplodon carlhubbsi* (Hubb's beaked whale); 32—*Mesoplodon europaeus* (Gervais' beaked whale); 33—*Mesoplodon ginkgodens* (ginkgo-toothed beaked whale); 34—*Mesoplodon mirus* (True's beaked whale); 35—*Mesoplodon perrini* (Perrin's beaked whale); 36—*Monodon monoceros* (narwhal); 37—*Neophocaena phocaenoides* (finless porpoise); 38—*Orcinus orca* (killer whale); 39—*Peponocephala electra* (melon-headed whale); 40—*Phocoena phocoena* (harbor porpoise); 41—*Phocoena sinus* (vaquita); 42—*Phocoena spinipinnis* (Burmeister's porpoise); 43—*Phocoenoides dalli* (Dall's porpoise); 44—*Physeter macrocephalus* (sperm whale); 45—*Platanista gangetica* (South Asian river dolphin); 46—*Pontoporia blainvillei* (franciscana); 47—*Pseudorca crassidens* (false killer whale); 48—*Sotalia fluviatilis* (tucuxi); 49—*Sotalia guianensis* (costero); 50—*Stenella attenuata* (pantropical spotted dolphin); 51—*Stenella coeruleoalba* (striped dolphin); 52—*Stenella frontalis* (Atlantic spotted dolphin); 53—*Stenella longirostris orientalis* (eastern spinner dolphin); 54—*Steno bredanensis* (rough-toothed dolphin); 55—*Tasmacetus shepherdi* (Shepherd's beaked whale); 56—*Tursiops aduncus* (Indo-Pacific bottlenose dolphin); 57—*Tursiops truncatus* (common bottlenose dolphin); 58—*Ziphius cavirostris* (Cuvier's beaked whale).

trait depend on transitions in the other. The dependent model has twice as many parameters to estimate as the independent model because each trait transition depends on two possible states in the other trait. These two models were compared using a likelihood ratio test (LRT), twice the difference in log-likelihoods compared to a X^2 distribution with four degrees of freedom (df; Pagel 1994).

Testing for the correlation of two categorical variables remains an unsolved challenge, as phylogenetic relatedness can lead to pseudoreplication of character state associations (Maddison and FitzJohn 2015). Worst case scenarios occur when one or both of the categorical variable states evolves once (or a few times), situations referred to as "Darwin's scenario" or "unreplicated bursts"

(Maddison and FitzJohn 2015). To qualitatively assess the sensitivity of our results to the problem of pseudoreplication, we report the number of times each state evolved and repeat the analyses in a number of ways (see below).

Results

Combined testes weights in our sample of 58 cetacean species ranged nearly five orders of magnitude, from 20 g in the franciscana (*Pontoporia blainvillei*; residual testes weight = −1.29) to over one ton in the North Pacific right whale (*Eubalaena japonica*; residual testes weight = 1.44; Table S1, Fig. 2). The estimated
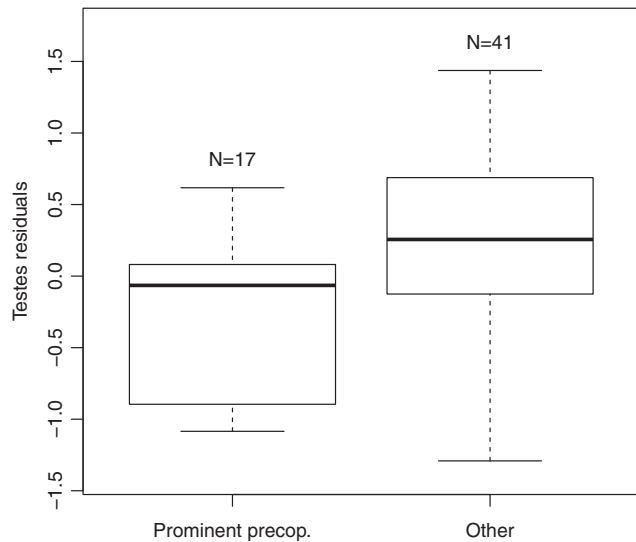
Figure 3. Residual testes mass across species groups. Thick horizontal line indicates median, box indicates interquartile range.

lambda from the PGLS of testes regressed onto maximum male body length was 0.84, significantly different than both lambda $= 0$ ($\chi^2 = 29.04$, $P < 10^{-7}$) and lambda $= 1$ ($\chi^2 = 7.4$, $P = 0.007$) which indicates phylogenetic signal is present in the data.

SSD was not phylogenetically correlated with residual testis mass (PGLS $F_{1,56} = 0.04$, $P = 0.84$, Fig. S2). The estimated lambda $= 0.84$ was significantly different than both lambda $= 0$ ($\chi^2 = 12.12$, $P = 0.0005$) and lambda $= 1$ ($\chi^2 = 4.84$, $P = 0.03$). This result did not change if we analyzed the two suborders of cetaceans separately (Mysticeti [baleen whales]: $F_{1,8} = 1.37$, $P = 0.28$; Odontoceti [toothed whales]: $F_{1,46} = 0.03$, $P = 0.86$).

Although SSD was not phylogenetically correlated with residual testis mass, the 17 species with prominent precopulatory phenotypes had significantly smaller residual testes than the remaining 41 species (Figs. 2, 3, PHYLANOVA $F = 8.54$, one-tailed $P = 0.007$). This result held if we analyzed Mysticeti separately (PHYLANOVA $F = 5.58$, one-tailed $P = 0.03$) and showed a strong but nonsignificant trend when we analyzed Odontoceti separately (PHYLANOVA $F = 4.92$, one-tailed $P = 0.07$).

The presence/absence of prominent precopulatory phenotypes was significantly correlated with the presence/absence of evidence that males may be able to monopolize access to females through contests (LRT $= 17.17$, df $= 4$, $P = 0.002$; Table S2). Eleven of 17 species with prominent precopulatory phenotypes showed evidence that males monopolize access to females through contest competition, compared to just five of the other 41 species (Table S2). Visual inspection of the distribution of precopulatory traits versus opportunity for monopolization suggest that beaked whales (the branches circled in red, Fig. S2) contribute disproportionately to the significance of this result. Therefore, we performed two additional analyses: one

after removing all beaked whale species except *Mesoplodon carlhubbsi* (leaving a single representative beaked whale species with both prominent precopulatory traits and opportunity for monopolization through contests) and one where we removed all beaked whale species except *Berardius bairdii* (leaving a single beaked whale species with neither). After including only *M. carlhubbsi*, the association remained significant (LRT $= 10.71$, $P = 0.03$), and was nearly significant after including only *B. bairdii* (LRT $= 8.62$, $P = 0.07$). In general, then, our result does not seem to be strongly driven by the beaked whales, consistent with a reasonable number of times each categorical trait evolved on the phylogeny. Prominent precopulatory traits evolved 10 independent times, and the opportunity for monopolization evolved eight independent times. Therefore, although these results should be treated with caution, they are not sensitive to the problematic "Darwin's scenario" or "unreplicated bursts" (Maddison and FitzJohn 2015). If we confined the analysis to a subset of 26 species with the strongest evidence (the "conservative set" in Table S2), the association between prominent precopulatory traits and the opportunity that males monopolize access to females remained significant (LRT $= 11.45$, df $= 4$, $P = 0.02$).

Discussion

When males are able to monopolize access to multiple females via contest competition, theory predicts a trade-off between investments in traits that are used in pre- versus postcopulatory sexual selection (Parker et al. 2013; Lüpold et al. 2014). Among all 58 cetacean species we analyzed here, SSD (a precopulatory trait) was not correlated to relative testes mass (a postcopulatory trait). Previous studies found that trade-off dynamics only hold for groups where male monopolization of access to females was common (Lüpold et al. 2014), suggesting that proportionately few cetacean species have such a mating system.

In many cetaceans, sexually receptive females are dispersed rather than aggregated during the breeding season, making it difficult for males to monopolize access to multiple females (Clutton-Brock 1989; Shuster and Wade 2003; Lukas and Clutton-Brock 2013). It is also likely more difficult for males to monopolize access to females in aquatic environments, where there is an additional axis of movement compared to terrestrial environments. It is interesting to note that the single aquatic group analyzed by Lüpold et al. (2014), the cyprinid minnows, did not show a trade-off between precopulatory and postcopulatory traits. Furthermore, Fitzpatrick et al. (2012) showed that the trade-off between precopulatory and postcopulatory traits in pinnipeds was driven by terrestrially breeding species that form harems, whereas the aquatically mating species did not show the same trade-off. Sexual selection in cetaceans may also favor small males that are more agile or maneuverable in scramble competition as has been suggested for mammals in which females are larger than males

Table 1. Trade-off between pre- and postcopulatory investment in male cetaceans.

	Testes residuals lower than expected (< mean residual − 0.5 SD)	Testes residuals as expected based body mass (within 0.5 SD of mean residual)	Testes residuals mass higher than expected (> mean residual + 0.5 SD)
A. Species with prominent precopulatory male traits	High precopulatory selection Low postcopulatory selection	High precopulatory selection Average postcopulatory selection	High precopulatory selection High postcopulatory selection
	*Mesoplodon ginkgodens** *Mesoplodon perrini** *Mesoplodon europaeus** *Mesoplodon carlhubbsi*** *Megaptera novaeangliae*** *Hyperoodon ampullatus*** *Monodon monoceros*** *Physeter macrocephalus***	*Balaenoptera musculus* *Lissodelphis borealis* *Balaenoptera physalus* *Phocoenoides dalli*** *Ziphius cavirostris*** *Globicephala melas* *Globicephala macrorhynchus*	*Stenella longirostris orientalis** *Orcinus orca*
B. Species without prominent precopulatory male traits	Low precopulatory selection Low postcopulatory selection	Low precopulatory selection Average postcopulatory selection	Low precopulatory selection High postcopulatory selection
	Pontoporia blainvillei *Lipotes vexillifer* *Mesoplodon mirus** *Tasmacetus shepherdi** *Caperea marginata* *Stenella coeruleoalba* *Delphinapterus leucas*	*Lagenorhynchus acutus* *Feresa attenuata* *Balaenoptera acutorostrata* *Balaenoptera edeni* *Balaenoptera borealis* *Tursiops truncatus** *Cephalorhynchus heavisidii* *Lagenorhynchus obliquidens* *Berardius bairdii* *Platanista gangetica* *Inia geoffrensis*** *Phocoena spinipinnis* *Tursiops aduncus*** *Peponocephala electra* *Cephalorhynchus commersonii* *Stenella frontalis*	*Eschrichtius robustus* *Steno bredanensis* *Stenella attenuata* *Pseudorca crassidens* *Neophocaena phocaenoides* *Cephalorhynchus hectori* *Kogia sima* *Phocoena sinus* *Sotalia fluviatilis* *Grampus griseus* *Kogia breviceps* *Sotalia guianensis* *Delphinus capensis* *Delphinus delphis* *Phocoena phocoena* *Balaena mysticetus* *Lagenorhynchus obscurus* *Eubalaena japonica*

Color coding indicating exaggerated male traits as in Figure 1. Evidence of potential male monopolization of access to females indicated by "**" using the "conservative" criteria and "*" using "relaxed" criteria (Table S2). Within each section, species are listed in increasing order, from smallest testes residuals (top) to largest testes residuals (bottom).

(Ralls 1976), birds (Andersson and Norberg 1981; Székely et al. 2000), and aquatically mating pinnipeds (Lindenfors et al. 2002; Fitzpatrick et al. 2012). Natural selection may favor large females that can better meet the demands of pregnancy, lactation, and long-distance migration or which can give birth to larger young (Ralls 1976). These possibilities may obscure a straightforward prediction about precopulatory versus postcopulatory investment.

In spite of the overall lack of a trade-off between SSD and relative testes mass among the 58 species, the 17 species with prominent precopulatory phenotypes had significantly smaller relative testes mass than the other 41 species. Furthermore, these

17 species are enriched for species males have an opportunity to monopolize access to females.

To examine the trade-off in more detail, we roughly divided species into thirds along the spectrum of relative testes mass (Table 1). Among species with prominent precopulatory phenotypes, the trade-off is strongest when males engage weaponry in direct combat (species in top left section of Table 1). Combat is expected to have a relatively large potential payoff (Parker et al. 2013) and the intensity of combat is predicted to scale with the probability of future mating opportunities (Enquist and Leimar 1990; Clapham 1996). The relative decrease in

investment in testes may be due to reduced resources remaining for allocation to postcopulatory traits, or because monopolization of females removes the opportunity for sperm competition (Lüpold et al. 2014). Species such as sperm whales, northern bottlenose whales, and some *Mesoplodon* species show strong evidence for direct male combat and also have some of the smallest relative testes mass (top left section, Table 1).

In contrast, the trade-off is weaker in species in which prominent precopulatory traits are more likely to be used as displays rather than in combat (top middle and right sections, Table 1). For example, there is no known evidence for male combat in killer whales, blue and fin whales, pilot whales, and eastern spinner dolphins. Their dimorphic characters appear to function as ornaments, rather than armaments. The lack of a trade-off with testes size suggests that males in these species are not able to monopolize access to females to the same extent as those with combat.

The majority of cetaceans lack prominent sexual dimorphism and show moderate or large testes (bottom middle and right sections, Table 1). These tend to be species without known evidence for male contests, and thus species in which males probably cannot monopolize access to multiple females. Exceptions include the aggressive interactions between male alliances and coercive herding of females in Indian Ocean bottlenose dolphins (*Tursiops aduncus*; Connor et al. 2000) and the potentially lethal battles in boto (*Inia geoffrensis*; Martin and Da Silva 2006). Lastly, a handful of species show little investment in either pre- or postcopulatory traits (bottom left section, Table 1). Included in this group is the one cetacean species considered to be monogamous, the franciscana (*P. blainvillei*), (Wells et al. 2013), in which evolution of large testes would not be necessary for sperm competition. Little is currently known of the mating systems of the other species listed in this section.

Two geographically distinct spinner dolphins offer a unique insight into the trade-off hypothesis. Adult males of the eastern spinner (*S. longirostris orientalis*, Fig. 1B) are highly sexually dimorphic, and in a large sample spanning multiple years, less than 1% achieve peak testes weights and epididymides full of sperm during the breeding season (Perrin and Mesnick 2003). In contrast, the whitebelly form, a hybrid between *S. l. orientalis* and Gray's spinner dolphin (*S. l. longirostris*), rarely exhibits prominent sexual dimorphism and approximately 15% of adult males have epididymides full of sperm during the breeding season (Perrin and Mesnick 2003). The smaller proportion of eastern subspecies males undergoing spermatogenesis is consistent with the hypothesis that sexually and socially dominant males control access to mating opportunities, at least to a larger degree than the whitebelly form. Consistent with trade-off theory, eastern form males have smaller relative testes size than the whitebelly males (Perrin and Mesnick 2003).

Conclusions

We found that a group of 17 cetacean species with prominent precopulatory phenotypes have relatively smaller testes than a group of 41 species without prominent precopulatory features. Our results are consistent with trade-off theory, despite limited available data on cetacean mating behavior. Eleven of the 17 species show evidence of male contests, which are often aggressive dominance interactions and which likely reflect the ability of winners to monopolize access to females.

Of course, studies of male traits can only provide partial insight into the complexities of male mating strategies and their interplay with natural and sexual selection. Phenotypic traits may not reflect important behavioral traits, such as the cooperative alliances among male Indian Ocean bottlenose dolphins (*T. aduncus*) and some common bottlenose dolphins (*Tursiops truncatus*; Connor et al. 2000). Futhermore, studies of the evolution of male traits fail to encompass coevolutionary dynamics between the mating strategies of both sexes (Bro-Jørgensen 2011; Ah-King et al. 2014). Almost nothing is known about how female cetaceans influence which males sire their calves, either through classic precopulatory female choice or postcopulatory mechanisms of cryptic female choice. Our study begins to paint a larger picture of the many possible male mating strategies and provides a foundation to predict mating systems for cetaceans.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Distribution of sexual size dimorphism.
Figure S2. Phylogenetic reconstruction of sexual size dimorphism (left) versus residual testes mass (right).
Table S1. A list of all species and data included in the study.
Table S2. Evidence that males use contest competition to monopolize access to females.