Sexual selection targets cetacean pelvic bones

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Male genitalia evolve rapidly, probably as a result of sexual selection. Whether this pattern extends to the internal infrastructure that influences genital movements remains unknown. Cetaceans (whales and dolphins) offer a unique opportunity to test this hypothesis: since evolving from land-dwelling ancestors, they lost external hind limbs and evolved a highly reduced pelvis that seems to serve no other function except to anchor muscles that maneuver the penis. Here, we create a novel morphometric pipeline to analyze the size and shape evolution of pelvic bones from 130 individuals (29 species) in the context of inferred mating system. We present two main findings: (1) males from species with relatively intense sexual selection (inferred by relative testes size) tend to evolve larger penises and pelvic bones compared to their body length, and (2) pelvic bone shape has diverged more in species pairs that have diverged in inferred mating system. Neither pattern was observed in the anterior-most pair of vertebral ribs, which served as a negative control. This study provides evidence that sexual selection can affect internal anatomy that controls male genitalia. These important functions may explain why cetacean pelvic bones have not been lost through evolutionary time.

KEY WORDS: Morphological evolution, sexual conflict, sexual selection.

The rapid divergence of male genitalia, probably the result of sexual selection affecting male–male competition and/or male–female interactions (Eberhard 1985; Dixson 1998; Hosken and Stockley 2004; Miller 2010), has emerged as a preeminent pattern in evolutionary biology. Male genitals may have evolved to remove sperm or otherwise reduce the fertility of competing males, to induce the female to accept insemination, to harm the female and inhibit her from remating, and/or to sneak matings (reviewed in Eberhard 1996; Simmons 2001; Arnqvist and Rowe 2005). Thus, male genitals are not solely involved in transfer of gametes, but participate in various arenas of competition and

conflict, the intensity of which is expected to intensify in relatively promiscuous species. Accordingly, male genitalia diverge more rapidly in more promiscuous species (Arnqvist 1998; Hosken and Stockley 2004; Ramm 2007), and some genital shapes are more effective at securing reproductive fitness under more competitive contexts (House and Simmons 2003, 2005; Stockley et al. 2013; Simmons and Firman 2014). One underlying mechanism for the divergence of male genitalia may be coevolution with the female. Over evolutionary time, selection may favor females that morphologically or behaviorally inhibit insemination, possibly as an indirect means to select the fittest mates from the population.
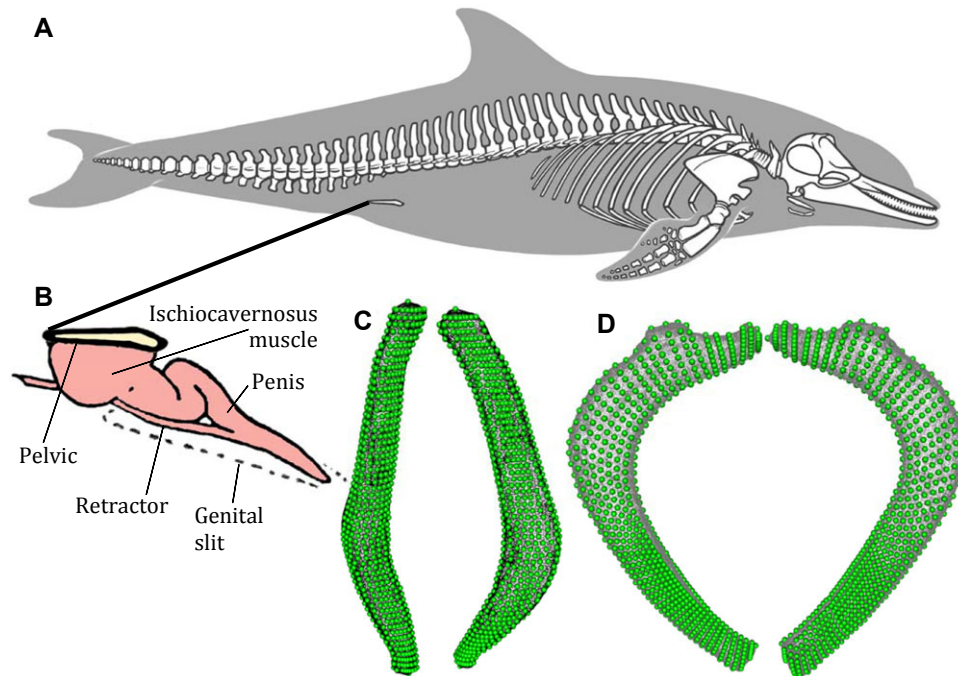
Figure 1. Skeletal anatomy of the bottlenose dolphin (*Tursiops truncatus*). **(A)** External hind limbs have been lost, and the pelvic girdle is reduced to a pair of small bones that no longer articulate with the skeleton—an adult male of approximately 3 m. *Source*: Carl Buell (used with permission from John Gatesy). **(B)** A closeup of the pelvic bone (cream colored), showing the soft tissue anatomy (pink). Labels indicate one of the paired ischiocavernosus muscles, the retractor penis muscle that holds the penis inside the body, and the genital slit of a male dolphin. Despite recent reports, the retractor penis muscle does not attach to the pelvic bone, and its sole function appears to be for holding the penis inside the body (Ommanney 1932); a male erection is therefore accompanied by relaxation of the retractor penis muscle, allowing the penis to extend outside the body. **(C)** Laser scans from paired pelvic bones (dorsal view, anterior toward top of figure) with 962 semilandmarks (green spheres; see Fig. S3 for more details). These pelvic bones are approximately 11 cm long. **(D)** Laser scans and semilandmarks (green spheres; see Fig. S4 for more details) from the anterior-most pair of ribs. These rib bones are approximately 14 cm long.

Selection may also favor males that counteract these measures, leading to a coevolutionary conflict of interest that drives divergence in both male and female reproductive anatomy (Baumgardner et al. 1982; Higginson et al. 2012).

In addition to genital morphology per se, selective processes could affect the way that males move their genitals in the events leading up to and including copulation, but this hypothesis remains largely unexplored. The pelvic bones of cetaceans (whales and dolphins) offer a unique opportunity to test this hypothesis. The ancestors of whales and dolphins were four-legged, land-dwelling mammals, "returning" to the aquatic environment roughly 54 million years ago (Gingerich et al. 1983, 1994; Bajpai and Gingerich 1998; Gingerich 2003; Uhen 2007a, b, 2010). Concomitant with the loss of external hind limbs and the evolution of streamlined fluke-powered swimming, the cetacean pelvic girdle evolved to a highly reduced state (Fig. 1A) over the span of roughly seven million years (Gatesy et al. 2013; McGowen et al. 2014). Cetacean pelves no longer share a symphysis at the sacrum, no longer contact the vertebral column, have lost their acetabulum and obturator foramen, and evolved to such small size that there

is still no general consensus as to which of the three fused bones found in their terrestrial ancestor (ischium, ilium, and pubis) they derive from (Cuvier 1823; Abel 1907; Lönnberg 1911; Lönnberg 1938; Yablokov et al. 1974; Tajima et al. 2004).

Due to their highly reduced state, cetacean pelvic bones are sometimes thought of as "useless vestiges" of their land-dwelling ancestry (Curtis and Barnes 1989). However, all 92 extant cetacean species except two (*Kogia sima* and *K. breviceps*, which appear to have replaced their pelvic bones with functional cartilaginous sheets, Benham 1901) have retained their pelvic bones. Furthermore, the anatomy of cetacean pelvic bones reveals important roles in male reproductive function. The paired pelvic bones anchor the genitalia and the paired ischiocavernosus muscles that control the penis (Struthers 1881; Delage 1885; Abel 1907; Meek 1918; Anthony 1922; Ommanney 1932; Slijper 1966; Pabst et al. 1998; Tajima et al. 2004; Rommel et al. 2007; Thewissen et al. 2009; Fig. 1B). In male cetaceans, the paired ischiocavernosus muscles insert deeply toward the distal end of the penis, while proximally encapsulating the paired crus of the penis that anchor to each pelvic bone (Ommanney 1932; Arvy 1978; De Guise

et al. 1994; Fig. 1B). The ischiocavernosus muscles appear to maneuver the penis by pulling it to one side or the other (Delage 1885) and may also maintain erection by compressing the corpus cavernosum proximally (Ommanney 1932). The ischiocavernosus muscles may work in conjunction with other soft tissue innovations to control the penis, but work in other systems suggests the ischiocavernosus muscles are fundamentally important in penis movements. In rats, surgically detaching the ischiocavernosus muscles results in severe penile dysfunction; males are unable to perform "flips" (rapid dorsiflexion of the penis) and as a result they cannot penetrate the vagina with their penis (Sachs 1982; Hart and Melese-D'Hospital 1983). In humans, anesthetizing the ischiocavernosus muscles results in a weaker erection (Claes et al. 1996).

The ischiocavernosus muscles attach to the pelvis in all mammals, but cetacean pelvic bones are unique because they are no longer constrained by sacral and hind limb attachments or by hind limb locomotion, potentially freeing them to diverge according to penis morphology. Penis length and control may evolve to counteract mating avoidance behavior. In at least some cetacean species, females will surface "belly-up" to avoid mating with coercive males. Male cetaceans can apparently maneuver their penises to overcome this female mating resistance behavior (Mate et al. 2005), and because penis length varies among marine mammals (Brownell and Ralls 1986; Fitzpatrick et al. 2012), the supporting pelvic bones may be an important part of male anatomy. Furthermore, cetacean penises lack a baculum (Slijper 1966; a bony os penis found in many mammals) as expected given its apparent flexibility.

Given evolutionary and anatomical evidence, we hypothesized that evolutionary patterns of cetacean pelvic bones have been driven by sexual selection, for instance via selection for larger penises, which would require larger ischiocavernosus muscles and their attachment sites. If sexual selection favors males that control their penises in novel ways, we also hypothesized that pelvic bone shape divergence (independent of size) would correlate to inferred mating system. We developed a novel morphometric pipeline to test these hypotheses using bones from 130 adult specimens taken from 29 species (Table S1), and report two main findings. First, cetaceans from relatively promiscuous mating systems (inferred by the well-established proxy of relative testes size, see below) have relatively long penises and relatively large pelvic bones, presumably to anchor relatively large ischiocavernosus muscles. Second, pelvic bone shape (independent of size) has diverged more in species pairs with larger inferred differences in mating system. Our study suggests that far from being mere relics of a terrestrial past, cetacean pelvic bones are targets of sexual selection.

Materials and Methods
ESTIMATING THE INTENSITY OF POSTCOPULATORY SEXUAL SELECTION ACROSS CETACEANS

Direct data on mating system are lacking for most cetaceans. Therefore, we indirectly estimated the strength of postcopulatory sexual selection from testes mass data gathered from the literature. Across a broad taxonomic diversity, males of species with relatively intense postcopulatory sexual selection tend to possess relatively large testes compared to their body size, including mammals (Harcourt et al. 1981; Kenagy and Trombulak 1986; Møller 1989; Stockley and Purvis 1993; Ramm et al. 2005; Firman and Simmons 2008; Simmons and Fitzpatrick 2012), fish (Stockley et al. 1997), and insects (Gage 1994; Hosken 2001; Simmons and García-González 2008). Large testes presumably represent a costly though adaptive trait as males vie for fertilization under competitive conditions. This pattern has been confirmed within species, among populations that differ in their inferred mating system (Firman and Simmons 2008), and upon experimental exposure to variable mating regimes (Hosken and Ward 2001; Pitnick et al. 2001).

In the modern era, most cetacean specimens come from beached animals in various states of degradation, so neither testes mass nor body mass can be reliably measured. Furthermore, testes regress outside of the breeding season. Therefore, we gathered maximum testes mass and body length from the literature for as many species as possible (Fig. 2, Table S2). Using the phylogeny of McGowen et al. (2009), we estimated the residuals of maximum testes mass regressed onto maximum body length using phylogenetic generalized least squares (PGLS) implemented via the generalized least squares (GLS) procedure in the R package (www.r–project.org) NLME, with a correlation structure that accounted for phylogenetic relatedness (Pagel 1999), using the corPagel procedure in the R package (APE; Paradis et al. 2004). Maximum body length was used as a proxy for body size rather than maximum body mass because most museum specimens derive from dead stranded individuals, and associated pathologies and/or decomposition render weight unreliable. The phylogenetic residuals of testes mass regressed onto body length (Figs. 2, S1) were used as a proxy of the strength of postcopulatory sexual selection within each species.

ANALYZING RELATIVE PENIS LENGTH

Using PGLS, we regressed penis length onto body length, using the data from Table 2 of Brownell and Ralls (1986), who reported on 10 baleen whale species. We then regressed the residuals of penis length onto testes mass residuals calculated above (Fig. S2).
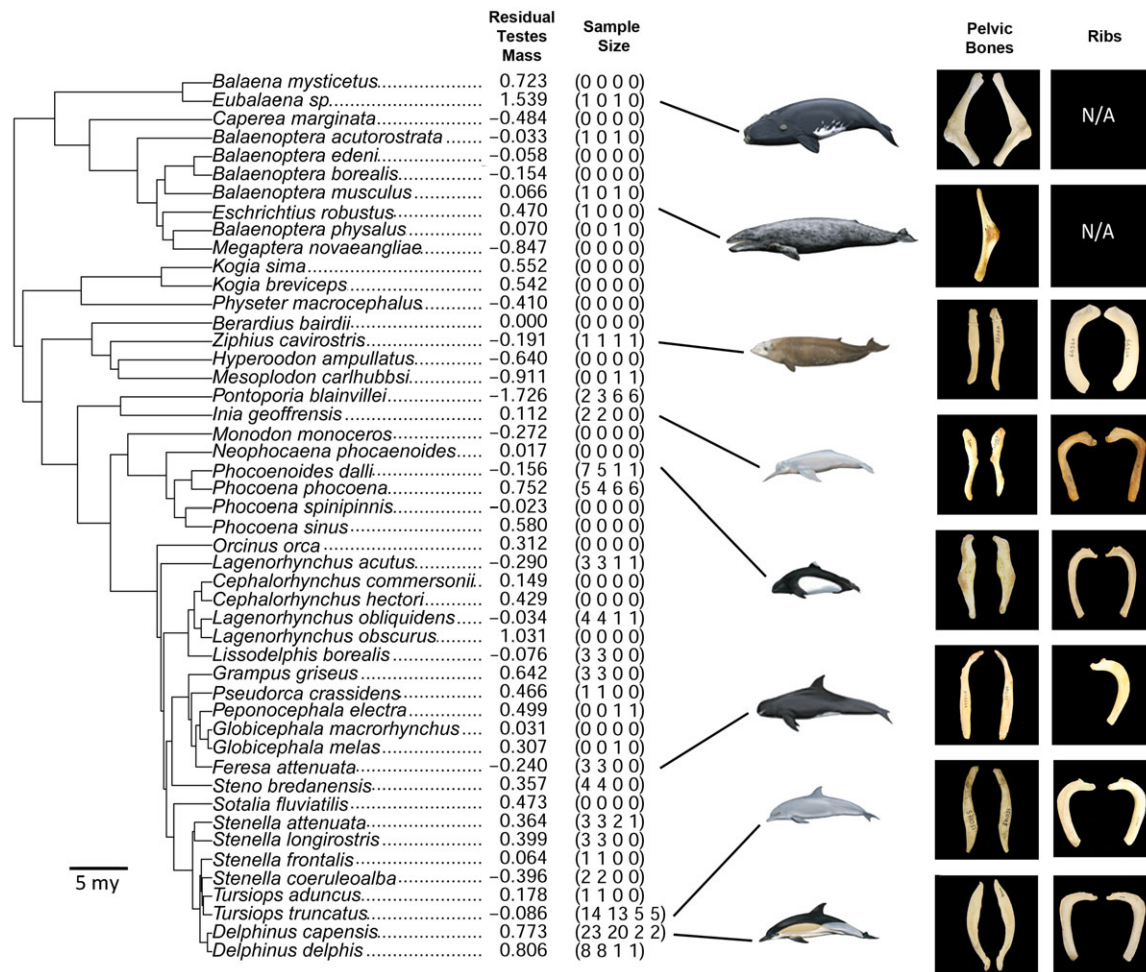
Species	Residual Testes Mass	Sample Size
Balaena mysticetus	0.723	(0 0 0 0)
Eubalaena sp.	1.539	(1 0 1 0)
Caperea marginata	−0.484	(0 0 0 0)
Balaenoptera acutorostrata	−0.033	(1 0 1 0)
Balaenoptera edeni	−0.058	(0 0 0 0)
Balaenoptera borealis	−0.154	(0 0 0 0)
Balaenoptera musculus	0.066	(1 0 1 0)
Eschrichtius robustus	0.470	(1 0 0 0)
Balaenoptera physalus	0.070	(0 0 1 0)
Megaptera novaeangliae	−0.847	(0 0 0 0)
Kogia sima	0.552	(0 0 0 0)
Kogia breviceps	0.542	(0 0 0 0)
Physeter macrocephalus	−0.410	(0 0 0 0)
Berardius bairdii	0.000	(0 0 0 0)
Ziphius cavirostris	−0.191	(1 1 1 1)
Hyperoodon ampullatus	−0.640	(0 0 0 0)
Mesoplodon carlhubbsi	−0.911	(0 0 1 1)
Pontoporia blainvillei	−1.726	(2 3 6 6)
Inia geoffrensis	0.112	(2 2 0 0)
Monodon monoceros	−0.272	(0 0 0 0)
Neophocaena phocaenoides	0.017	(0 0 0 0)
Phocoenoides dalli	−0.156	(7 5 1 1)
Phocoena phocoena	0.752	(5 4 6 6)
Phocoena spinipinnis	−0.023	(0 0 0 0)
Phocoena sinus	0.580	(0 0 0 0)
Orcinus orca	0.312	(0 0 0 0)
Lagenorhynchus acutus	−0.290	(3 3 1 1)
Cephalorhynchus commersonii	0.149	(0 0 0 0)
Cephalorhynchus hectori	0.429	(0 0 0 0)
Lagenorhynchus obliquidens	−0.034	(4 4 1 1)
Lagenorhynchus obscurus	1.031	(0 0 0 0)
Lissodelphis borealis	−0.076	(3 3 0 0)
Grampus griseus	0.642	(3 3 0 0)
Pseudorca crassidens	0.466	(1 1 0 0)
Peponocephala electra	0.499	(0 0 1 1)
Globicephala macrorhynchus	0.031	(0 0 0 0)
Globicephala melas	0.307	(0 0 1 0)
Feresa attenuata	−0.240	(3 3 0 0)
Steno bredanensis	0.357	(4 4 0 0)
Sotalia fluviatilis	0.473	(0 0 0 0)
Stenella attenuata	0.364	(3 3 2 1)
Stenella longirostris	0.399	(3 3 0 0)
Stenella frontalis	0.064	(1 1 0 0)
Stenella coeruleoalba	−0.396	(2 2 0 0)
Tursiops aduncus	0.178	(1 1 0 0)
Tursiops truncatus	−0.086	(14 13 5 5)
Delphinus capensis	0.773	(23 20 2 2)
Delphinus delphis	0.806	(8 8 1 1)

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Pelvic Bones / Ribs (N/A, rib bones could not be sampled from all museum specimens)

Figure 2. Phylogeny of cetacean taxa (adapted from McGowen et al. 2009) with known maximum testes size and body length. Residual testes mass calculated as described in Figure S1. Sample size indicates the number of individuals sampled for male pelvic, male rib, female pelvic, and female rib bones, respectively. Images indicate representative body morphology (left column; *source*: Carl Buell [used with permission from John Gatesy]), paired pelvic bones (middle column), and paired rib bones (right column) from a subset of species. N/A, rib bones could not be sampled from all museum specimens. For *Eubalaena* sp. testis and body length from *Eubalaena japonica*, pelvic bone from *Eubalaena glacialis*. There are no known morphological differences between the two species (Rice 1998; Jefferson et al. 2008), which were only recently recognized as genetically distinct (Rosenbaum et al. 2000).

DEFINING SEMI-LANDMARKS ON BONES

From museum collections, we gathered pelvic bones from 97 sexually mature males (24 species) (Fig. 2, Table S1). Where possible (87 sexually mature males from 20 species), we included the anterior-most pair of vertebral ribs as a negative control as they are not linked to genital musculature (Fig. 2, Table S1). It should be noted that some cetacean species retain internal vestiges of femora and/or tibiae (Struthers 1881; Howell 1970; Omura 1980) and in extremely rare cases individuals develop external hind limbs (Andrews 1921; Sleptsov 1939; Ohsumi 1965; Berzin 1972). However, these additional bones do not attach to the ischiocavernosus muscles and are ignored here.

Cetacean pelvic bones are devoid of distinguishing landmarks (Fig. 1C), hampering traditional morphometric techniques.

To overcome these challenges, we first scanned bones with a NextEngine HD Model 2020i three-dimensional Laser Scanner (NextEngine, Inc., Santa Monica, CA), which returns tens of thousands of *x*, *y*, *z* points from the surface of each bone. Using a variety of tools in computational geometry, we defined 962 semilandmarks from digitized versions of the bones for downstream analyses (Fig. 1C and 1D). This computational pipeline is graphically illustrated for pelvic bones (Fig. S3) and ribs (Fig. S4) separately.

It is important to consider the female side of sexual selection (Ah-King et al. 2014). As in males, female ischiocavernosus muscles originate on the pelvic bone, but insert instead on the clitoris. There are at least three predictions about how female pelvic bones should evolve. First, female pelvic bones may show no

relationship to relative testes mass of their species, for example, if female pelvic bones are nonfunctional. Second, even if female pelvic bones are nonfunctional, they may follow the patterns observed in males simply through shared developmental programs. Third, females may experience their own unique selective pressures associated with pelvic bones if they are functional. We tested these predictions by repeating the above analyses on female pelvic (33 sexually mature females from 17 species) and rib (27 females from 12 species) bones (Fig. 2, Table S1).

THE EVOLUTION OF BONE SIZE

Bone size was estimated with centroid size, the square root of the sum of squared distances of the 962 semilandmarks from their centroid. We quantified technical replication by randomly choosing 41 bones (21 pelvic bones, 20 ribs) to scan more than once. One bone was scanned 11 times, the rest scanned twice, each time removing the bone from the scanner and reloading it. The median coefficient of variation (unbiased SD/mean) for centroid size was 0.0094 for pelvic bones and 0.0090 for ribs, indicating our methods of measuring size were highly repeatable.

Two different analyses were performed to test whether bone size evolved in a correlated manner with residual testes mass. First, we calculated the phylogenetic residuals of species-averaged centroid size regressed onto species-averaged body length, then tested whether those residuals were correlated to testes mass residuals, all using PGLS methodology already described.

The simple application of PGLS ignored several complexities in the data, including missing data (not all target bones are present in museum collections) and uneven sampling of species (Table S1). Furthermore, as a correlation between residual pelvic size and residual testes mass, the underlying model is not clear. Therefore, we developed a second, customized phylogenetic model to explicitly test correlated trait evolution (Harmon et al. 2008) in which log body length, testes size, and left and right pelvic and rib centroid sizes evolve as a multivariate Brownian motion on the cetacean phylogeny (McGowen et al. 2009), with individual samples displaced by independent amounts from their species means. This is a standard model of correlated trait evolution (Revell and Collar 2009) except for explicit modeling of intraspecific variation and missing data. To perform Bayesian inference, we placed zero-mean Gaussian priors on the entries of the Cholesky decomposition of the covariance matrix and ran a Markov Chain Monte Carlo sampler to estimate the posterior distribution of the parameters. The mathematical details and parameter estimates appear in Supporting Information Materials and Methods.

THE EVOLUTION OF BONE SHAPE

We quantified shape difference between all possible pairs of pelvic bones, and between all possible pairs of rib bones in a Generalized Procrustes framework, which standardizes each set of 962 semilandmarks to a common size, translates them to a common origin, then optimally rotates semilandmark coordinates to minimize their Procrustes distance, which is the square root of the sum of the squared distances between corresponding landmarks (Rohlf and Bookstein 1990; Slice 2007). During Procrustes superimposition, our semilandmarks were allowed to "slide" along the bones' surfaces using the function GPAGEN in the R package GEOMORPH (Adams and Otárola-Castillo 2012). Sliding semilandmarks is a well-established morphometric technique used to improve alignment of corresponding anatomical regions lacking individual landmark homology (Bookstein 1996, 1997; Gunz et al. 2005; Mitteroecker and Gunz 2009). In short, sliding semilandmarks accompanies uncertainty in specific placement of landmarks. Left-sided bones were reflected prior to aligning.

Technical replication was estimated using the same rescans described above. The median coefficient of variation for shape differences between each rescan and all the other bones in the sample was 0.0194 for pelvic bones and 0.0342 for ribs, indicating our methods for measuring shape divergence were highly repeatable.

SEXUAL DIMORPHISM

All analyses described above were performed for males and females separately. In addition, four different distance-based analyses of variance (ANOVAs; McArdle and Anderson 2001) were performed to test the contribution of sex to variance in pelvic or rib bones size or shape, using the function ADONIS in the R package VEGAN (Oksanen et al. 2013), with significance determined with 10,000 permutations.

Results

ESTIMATING THE INTENSITY OF POSTCOPULATORY SEXUAL SELECTION ACROSS CETACEANS

All else equal, species with larger testes mass residuals are expected to experience a more promiscuous mating system. This prediction has been confirmed in multiple systems (see above), and aligns well with the scant amount of independent data on mating system in cetaceans. For example, *Pontoporia blainvillei* (the franciscana) has the smallest absolute and residual testes mass (Table S2), and is thought to be monogamous (Danilewicz et al. 2004). In contrast, direct behavioral and genetic observations suggest three species—*Eubalaena glacialis* (North Atlantic right whale; Mate et al. 2005; Frasier et al. 2007; Frasier et al. 2013), *Balaena mysticetus* (bowhead whale; Würsig and Clark 1993), and *Lagenorhynchus obscurus* (the dusky dolphin; van
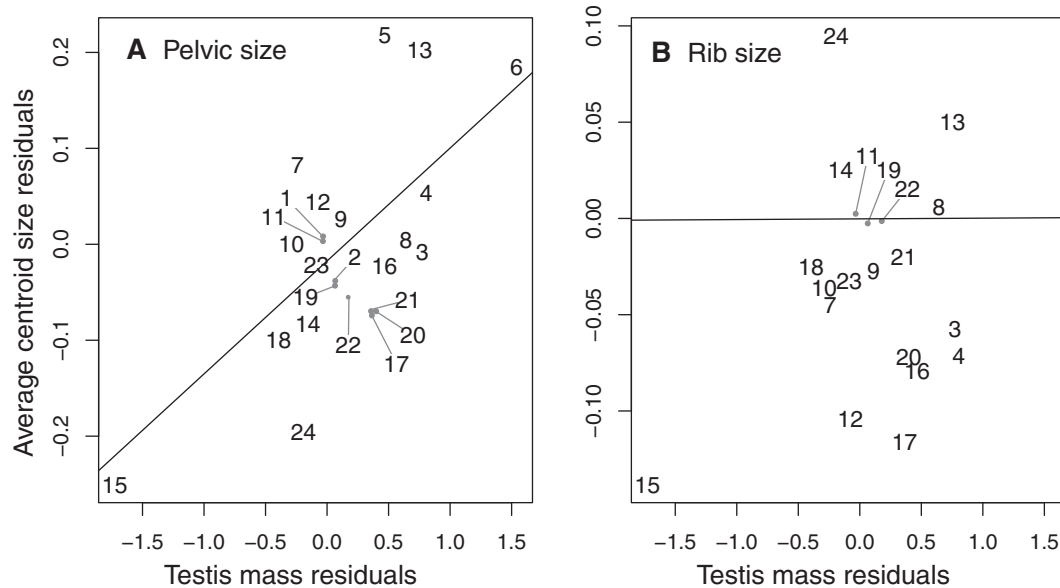
Figure 3. Among sexually mature males, residual centroid size (species-average centroid size regressed onto body length) was positively correlated with residual testes mass (using PGLS methodology) in (A) pelvic bones, but not (B) ribs. Species: 1, *Balaenoptera acutorostrata*; 2, *B. musculus*; 3, *Delphinus capensis*; 4, *D. delphis*; 5, *Eschrichtius robustus*; 6, *Eubalaena* sp. 7, *Feresa attenuata*; 8, *Grampus griseus*; 9, *Inia geoffrensis*; 10, *Lagenorhynchus acutus*; 11, *L. obliquidens*; 12, *Lissodelphis borealis*; 13, *Phocoena phocoena*; 14, *Phocoenoides dalli*; 15, *Pontoporia blainvillei*; 16, *Pseudorca crassidens*; 17, *Stenella attenuata*; 18, *S. coeruleoalba*; 19, *S. frontalis*; 20, *S. longirostris*; 21, *Steno bredanensis*; 22, *Tursiops aduncus*; 23, *T. truncatus*; 24, *Ziphius cavirostris*.

Waerebeek and Read 1994)—are promiscuous, and all three have large absolute and residual testes (Table S2).

RELATIVE PENIS LENGTH INCREASES WITH RELATIVE TESTIS MASS

Species with large relative testes mass have significantly larger penises compared to their body length (phylogenetically controlled $P < 10^{-4}$, $r = 0.65$, Fig. S2). Although the ultimate mechanism behind this correlation is not clear, one possibility is that males with longer penises can better overcome female resistance behavior in relatively promiscuous species, behaviors that were observed by Mate et al. (2005). Or perhaps female reproductive tracts are more convoluted in more promiscuous species, favoring males that can deposit sperm closer to the sites of fertilization. Longer genitalia in relation to sexual selection has been observed in other mammalian taxa (Miller and Burton 2001; Lüpold et al. 2004; Kinahan et al. 2007; Fitzpatrick et al. 2012). Whatever the underlying cause, we hypothesized that species with relatively large testes must have relatively large ischiocavernosus muscles to control their relatively large penises, which in turn require relatively large pelvic bones to serve as anchors. We note that the penis length data only derive from baleen whales (Fig. S2). Any uncertainty about the relationship between residual testes mass and residual penis length in toothed whales will only introduce noise into our studies of correlated trait evolution across the full phylogeny, making our conclusions below conservative.

RELATIVE SIZE OF PELVIC BONES INCREASES WITH RELATIVE TESTIS MASS

Two different methods demonstrated that pelvic bone size increased along with testes mass. First, using PGLS methodology, relative pelvic size (log pelvic bone centroid size phylogenetically regressed onto log body length per specimen, averaged per species, Fig. S5) was positively correlated with relative testes mass (phylogenetically controlled, $P = 0.0006$, $r = 0.55$, Fig. 3A), a pattern not observed in ribs (phylogenetically controlled, $P = 0.98$, $r = 0.01$, Figs. 3B, S6). A Q–Q plot identified three outlier species (*Ziphius cavirostris*, *Feresa attenuata*, *Eschrichtius robustus*) that contributed disproportionately to the regression (Fig. 3A), but the PGLS was still significant after removing them (phylogenetically controlled $P < 10^{-4}$, $r = 0.70$). The PGLS was also significant if we confined the analysis to those specimens for which both pelvic and rib data existed (phylogenetically controlled $P = 0.008$, $r = 0.54$).

Second, our customized phylogenetic model demonstrated that after removing their common correlation to body length, male pelvic bone centroid sizes were positively correlated to testes mass (correlation $\rho = 0.67$, 95% credible interval: 0.25–0.90, Fig. 4A, Tables S3 and S4). In other words, species with relatively large
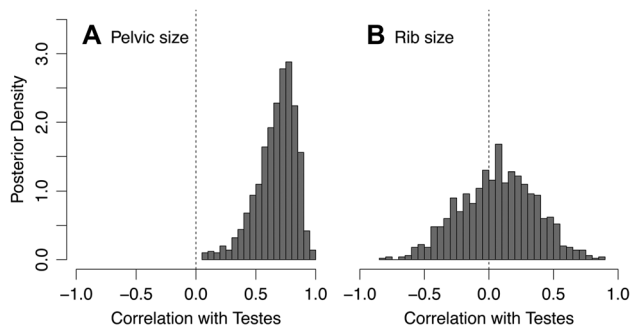
Figure 4. The results of a customized Bayesian model of correlated evolution between traits. (A) All 1000 correlation coefficients sampled from the marginal posterior distribution showed that shifts in relative testes mass positively predicted shifts in pelvic centroid size (posterior mean correlation ρ = 0.67, 95% credible interval: 0.25–0.90). (B) In contrast, shifts in testes size did not predict shifts in rib centroid size (posterior mean correlation ρ = 0.05, 95% credible interval: −0.38 to 0.48).

testes tend to evolve larger pelvic bones relative to their body length. There was no correlation between rib centroid size and testes size (correlation ρ = 0.07, 95% credible interval: −0.51 to 0.62, Fig. 4B, Tables S3 and S4). Results were qualitatively similar if we only analyzed those individuals represented in both the pelvic and the rib datasets (Fig. S7), although we narrowly lose statistical significance at 95% for the correlation between pelvic bone centroid size and testes (correlation ρ = 0.58, 95% credible interval: −0.05 to 0.92, Tables S5 and S6).

To limit the ecological variation across the full phylogeny, and to specifically focus on species where intraspecific variation could be estimated, we reanalyzed two independent species pairs with relatively large sample sizes: *Phocoena phocoena* (N = 5 sexually mature males) versus *Phocoenoides dalli* (N = 8) and *Delphinus capensis* (N = 23) versus *D. delphinus* (N = 7). For both species pairs, residual pelvic bone centroid size was significantly larger in the species with the larger residual testes size (t = 8.77, 3.40; degrees of freedom [df] = 10, 29; $P < 10^{-5}$, 0.002 for the two species pairs, respectively), a pattern not observed in ribs (t = 1.23, 1.08; df = 7, 26; P = 0.26, 0.29, respectively). The two *Delphinus* species are so closely related that they were only recognized as separate species 20 years ago (Heyning and Perrin 1994); even in this species pair, the taxon with the larger residual testes size displayed larger residual pelvic bone size.

In sum, cetaceans with relatively large testes have relatively large pelvic bones, but not ribs. Relatively large pelvic bones provide more surface area for attachment of the ischiocavernosus muscles, offering one mechanism by which males could achieve enhanced maneuverability of relatively large penises.

PELVIC BONE SHAPE DIVERGES MORE RAPIDLY AMONG SPECIES THAT HAVE DIVERGED IN INFERRED MATING SYSTEM

Among ten independent species pairs for which both pelvic bones and rib bones could be analyzed, pelvic bone shape divergence (independent of size) was positively correlated with divergence in inferred mating system (Pearson's correlation P = 0.003, r = 0.82, Fig. 5A). As with the analyses of size presented above, such a relationship did not hold for ribs (Pearson's correlation P = 0.98, r = −0.009, Fig. 5B), demonstrating a unique link between inferred mating system and pelvic bone shape evolution.

SEXUAL DIMORPHISM

Interestingly, female pelvic bone centroid size residuals were positively correlated with residual testes mass of their species, in both the PGLS and the customized phylogenetic models described (PGLS: P = 0.0052, r = 0.64, Fig. S8; customized model: ρ = 0.77, 95% credible interval: 0.30–0.99, Fig. S9, Tables S7 and S8), a pattern not observed in ribs (PGLS: P = 0.94, r = −0.10, Fig. S8; customized model: ρ = 0.20, 95% credible interval: −0.58 to 0.80, Fig. S9, Tables S7 and S8), just as observed in males. In other words, pelvic bones are relatively large in females of species that have males with relatively large testes.

The similarity of evolutionary patterns observed in males and females could be due to shared developmental programs. However, both pelvic bones and ribs were significantly sexually dimorphic in both size and shape ($P < 0.05$ in all cases, Tables S9 and S12), consistent with previous reports (van Bree 1973; Perrin 1975; Arvy 1979; Andersen et al. 1992). Taken together, these results suggest that pelvic bones function in unique aspects of male and female reproductive ecology. As discussed above, pelvic bones anchor ischiocavernosus muscles in females, which insert on the clitoris. It is possible that clitoral movements play a role in female choice, potentially placing the female pelvic bone in the arena of sexual selection. At the moment this hypothesis remains speculative.

Discussion

Under certain models, sexual selection favors females that make it difficult—behaviorally, morphologically, or otherwise—for males to fertilize their ova, which subsequently favors males that overcome these defenses (Eberhard 1985; Andersson 1994; Eberhard 2009). Such mechanisms may yield indirect benefits to females through acquisition of good genes for her progeny and/or her ability to produce competitive sons. The strength of such coevolutionary dynamics is expected to intensify in relatively promiscuous species. For example, genital morphology evolves relatively rapidly in promiscuous versus monogamous species
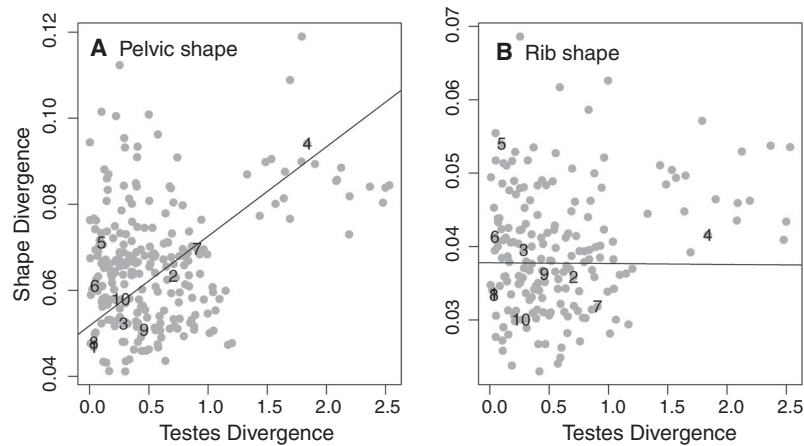
Figure 5. (A) Among nine independent species pairs, pelvic bone shape divergence was positively correlated with divergence in testes residuals ($P = 0.003$, $r = 0.82$). (B) In contrast, rib shape divergence was not correlated with divergence in testes size residuals ($P = 0.98$, $r = -0.009$). For completeness, the data for all species pairs, including nonindependent comparisons, is shown in gray circles, although they were not included in tests of correlation. Only sexually mature males for which both pelvic and rib bones could be sampled were included; species pairs: 1, *Delphinus capensis* versus *D. delphis*; 2, *Feresa attenuata* versus *Pseudorca crassidens*; 3, *Grampus griseus* versus *Steno bredanensis*, 4, *Inia geoffrensis* versus *Pontoporia blainvillei*, 5, *Lagenorhynchus acutus* versus *Ziphius cavirostris*; 6, *L. obliquidens* versus *Lissodelphis borealis*; 7, *Phocoenoides dalli* versus *Phocoena phocoena*; 8, *Stenella attenuata* versus *S. longirostris*; 9, *S. coeruleoalba* versus *S. frontalis*; 10, *Tursiops aduncus* versus *T. truncatus*.

(Arnqvist 1998). In the context of cetaceans, female avoidance behavior may induce selection on males to overcome such defenses. Because direct observations of cetacean mating behavior are scant, this hypothesis remains speculative. However, males have been observed to counteract female avoidance behavior through dexterous control of their penises (Mate et al. 2005).

Across the cetacean phylogeny, both size and shape of pelvic bones are evolutionarily correlated to relative testes mass, a strong indication of the strength of postcopulatory sexual selection (Harcourt et al. 1981; Kenagy and Trombulak 1986; Møller 1989; Gage 1994; Stockley et al. 1997; Hosken 2001; Ramm et al. 2005; Firman and Simmons 2008). One unifying hypothesis is that cetaceans that experience strong sexual selection have evolved relatively large penises that require relatively large muscles and pelvic bones to serve as anchor sites for genital control. Sexual selection also appears to favor divergence in shape, perhaps allowing males to maneuver their penises in novel ways. Importantly, our study rejects a common assumption (mostly among noncetacean biologists) that cetacean pelvic bones are "useless vestiges" (Curtis and Barnes 1989), and instead suggest they are a critical component of male, and possibly female, reproductive fitness. To our knowledge, this is the first example of sexual selection affecting the internal infrastructure affecting genital movements.

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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. The regression of maximal recorded testis size onto maximal recorded body length.
Figure S2. Whale species with relatively large testes have relatively long penises.
Figure S3. A series of tools in computational geometry were deployed to define landmarks from pelvic bone scans.
Figure S4. A series of tools in computational geometry were deployed to define landmarks from rib bone scans.
Figure S5. Species–averaged pelvic centroid sizes regressed onto species–averaged body length.
Figure S6. Species–averaged rib centroid sizes regressed onto species–averaged body length.
Figure S7. The marginal posterior distributions of correlation coefficients do not change when restricting to bones from adult male cetaceans for which we have both data for both ribs and pelvic bones.
Figure S8. As in males (see Fig. 3 of manuscript), among sexually mature females, residual centroid size (species-average centroid size regressed onto body length) was positively correlated with residual testes mass of males from their species (maximum species testes mass regressed onto maximum body length) in (A) pelvic bones, but not (B) ribs.
Figure S9. As observed for males (Fig. 4 of manuscript), the marginal posterior distributions of correlations between changes in female pelvic bone size was significantly correlated with shifts toward larger testis size.
Table S1. Individual level data from bone scans.
Table S2. Morphological data gathered from literature for sexually mature males.
Table S3. Posterior means and quantiles of the parameters of the model presented in equations (7) and (8) of supplemental methods, estimated using only bones from adult males.
Table S4. Marginal posterior distributions of correlations, with length fixed, between changes in rib size, pelvic bone size, and testes size, estimated using only bones from adult males.
Table S5. Posterior means and quantiles of the parameters given the dataset consisting only of bones from males for which we have both ribs and pelvic bones.
Table S6. Marginal posterior distributions of correlations, with length fixed, between changes in rib size, pelvic bone size, and testes size, given only data for bones in males for which we have both ribs and pelvic bones.
Table S7. Posterior means and quantiles of the parameters, for bones from females only.
Table S8. Correlations from females: marginal posterior distributions of correlations, with length fixed, between changes in rib size, pelvic bone size, and testes size, given bones from females only.
Table S9. Distance-based ANOVA of pairwise differences in pelvic bone centroid size.
Table S10. Distance-based ANOVA of pairwise differences in rib bone centroid size.
Table S11. Distance-based ANOVA of pairwise differences in pelvic bone shape.
Table S12. Distance-based ANOVA of pairwise differences in rib bone shape.