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MALE CONTEST COMPETITION AND THE COEVOLUTION OF WEAPONRY AND TESTES IN PINNIPEDS

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Male reproductive success is influenced by competitive interactions during precopulatory and postcopulatory selective episodes. Consequently, males can gain reproductive advantages during precopulatory contest competition by investing in weaponry and during postcopulatory sperm competition by investing in ejaculates. However, recent theory predicts male expenditure on weaponry and ejaculates should be subject to a trade-off, and should vary under increasing risk and intensity of sperm competition. Here, we provide the first comparative analysis of the prediction that expenditure on weaponry should be negatively associated with expenditure on testes mass. Specifically, we assess how sexual selection influences the evolution of primary and secondary sexual traits among pinnipeds (seals, sea lions, and walruses). Using recently developed comparative methods, we demonstrate that sexual selection promotes rapid divergence in body mass, sexual size dimorphism (SSD), and genital morphology. We then show that genital length appears to be positively associated with the strength of postcopulatory sexual selection. However, subsequent analyses reveal that both genital length and testes mass are negatively associated with investment in precopulatory weaponry. Thus, our results are congruent with recent theoretical predictions of contest-based sperm competition models. We discuss the possible role of trade-offs and allometry in influencing patterns of reproductive trait evolution in pinnipeds.

KEY WORDS: Contest competition, ejaculate allocation, genital evolution, sexual selection.

Understanding reproductive trait evolution requires a holistic approach that assesses competition during both precopulatory and postcopulatory episodes of sexual selection (Preston et al. 2003; Schulte-Hostedde et al. 2011; Parker et al. 2012). Darwin (1871) recognized that individuals (usually males) who invest in "weapons" (e.g., large body size, horns, or antlers) are at a competitive advantage during precopulatory episodes of sexual selection. There is now considerable evidence that increased investment in such weaponry enhances a male's competitive ability in species where male–male (contest) competition governs access to females (Andersson 1994). Yet, in many species male–male competition continues after mating in the form of sperm competition, when sperm from rival males compete to fertilize a females' eggs (Parker 1970), and females can influence the outcome of this competition by exerting cryptic female choice (Eberhard 1996). Consequently, a male's reproductive success also depends on his ejaculate and genital traits relative to those of rival males (Martin et al. 1974; Birkhead et al. 1999; Gage et al. 2004; Denk et al. 2005; García-González 2008; Simmons et al. 2009; Gasparini et al. 2010; Evans et al. 2011). Thus, male reproductive success is influenced by competitive interactions during both pre- and postcopulatory selective episodes. However, maximizing investment in traits that are beneficial both before and after mating can be problematic as weapons and reproductive traits used in pre- and postcopulatory male-male competition are energetically expensive (Dewsbury 1982; Solberg and Saether 1993; Olsson et al. 1997; Moen et al. 1999; Emlen 2001; Larivière and Ferguson 2002; Allen and Levinton 2007) and the amount of energy that a male can allocate to these traits is typically fixed during a given reproductive episode (i.e., from investment in pre- and postcopulatory traits through to mating). Therefore, investment in precopulatory weapons is predicted to limit investment in reproductive traits that enhance postcopulatory competitive success (Parker et al. 2012).

Previous game theoretic models of ejaculate expenditure have implicitly assumed that increased expenditure on acquiring mates reduces a males ability to allocate energy to his ejaculate (reviewed by Parker and Pizzari 2010). These previous models are based on the idea that males scramble for access to mates and predict an increase in expenditure on the ejaculate with increased risk of sperm competition (Parker and Pizzari 2010). More recently, Parker et al. (2012) developed a general model of sperm allocation that explores how different forms of male competition, and in particular male expenditure on weaponry for direct combat, might influence the predicted ejaculate expenditure. A general prediction of this new model is that expenditure on precopulatory traits limits expenditure on postcopulatory traits and vice versa (Parker et al. 2012). Thus, for any given level of sperm competition risk, expenditure on the ejaculate is expected to decrease and expenditure on weaponry is expected to increase as the marginal mating gains from investing in contest competition increase (Parker et al. 2012).

There is some evidence to suggest a negative relationship between weapons and reproductive traits from a variety of species (reviewed by Parker et al. 2012). For example, direct evidence of a trade-off between weapons and testes comes from the dung beetle *Onthophagus nigriventris*, where males that were experimentally prevented from developing horns (used in male–male competition for access to tunnels used by breeding females) invested greater resources in testicular tissue (Simmons and Emlen 2006). Likewise, in the congeneric beetle *O. taurus*, males experimentally prevented from developing external genitalia invested in longer horns (Moczek and Nijhout 2004). In addition, in the domestic fowl (*Gallus gallus domesticus*) and Arctic charr (*Salvelinus alpinus*), two species where males form social dominance hierarchies but where social status is flexible, sperm quality declined in males that ascend to a socially dominant position after agonistic dyadic interactions (Rudolfsen et al. 2006; Pizzari et al. 2007). Thus, the costs associated with securing social dominance appear to limit subsequent investment in ejaculate traits. Unfortunately, there is considerably less evidence in support of Parker et al.'s (2012) prediction of a negative relationship between expenditure on pre- and postcopulatory traits in cases where the risk of sperm competition varies across populations or species. Thus far, the best evidence of such a trade-off comes from the myobatrachid frog *Crinia georgiana*, a species where male density at choruses, and the associated risk of sperm competition, varies among populations (Roberts et al. 1999; Byrne and Roberts 2004). In a comparison of 10 populations, Parker et al. (2012) reported that males had larger forelimbs, which are used during male–male disputes over territorial ownership (Howard 1978), and smaller testes when the risk of sperm competition was low. In contrast, male *C. georgiana* invested more in testes mass and less in forelimb size in populations where the risk of sperm competition was elevated (Parker et al. 2012). However, there has yet to be an interspecific examination of how variance in male–male competition covaries with investment in traits that determine fitness during pre- and postcopulatory episodes of sexual selection.

In this study, we investigate how sexual selection influences the evolution of reproductive traits and assess the relationship between expenditure on traits important in precopulatory male–male competition and postcopulatory sexual selection among pinnipeds (seals, sea lions, and walruses). Pinnipeds are an ideal model system to contrast investment in pre- and postcopulatory traits as differences in breeding sites among pinnipeds generates dramatic variance in the strength of sexual selection, the prevalence of male–male contest competition, and investment in weaponry used in contest competition (Bartholomew 1970; Lindenfors et al. 2002). Ice-breeding species, which typically engage in aquatic matings, are primarily socially and/or serially monogamous (although there is scope for sperm competition, e.g., Kovacs 1995), as in these species breeding areas are not limited and females are not defendable (Stirling 1983; Le Boeuf 1991). The exact opposite is the case in species of land-breeding pinnipeds, where females aggregate on beaches during the breeding season and males attempt to monopolize breeding areas through intense male–male competition (Boness 1991). In these land-breeding species, larger males are more successful during male–male competition and have greater reproductive success (Le Boeuf 1974; McCann 1981; Deutsch et al. 1990; Tinker et al. 1995; Modig 1996; Arnould and Duck 1997) leading to intense precopulatory selection for increased male body size and a positive relationship between the degree of sexual size dimorphism (SSD) and harem size (Alexander et al. 1979; Lindenfors et al. 2002). Yet, while it is clear that precopulatory competition plays an important role in shaping male weaponry (in this case large body sizes), much less is known about how selection acts on traits important in postcopulatory sexual selection in pinnipeds, or the nature of the relationship between traits influenced by these two episodes of sexual selection. Therefore, we begin by assessing evolutionary responses in traits important in pre- and postcopulatory competition by contrasting rates of phenotypic divergence in species where males experience different forms of competition and thus varying levels of sexual selection. Next, we investigate how sperm competition influences the evolution of genital length in pinnipeds. Although there is clear evidence that male genital morphology evolves rapidly in response to variation in the strength of postcopulatory sexual selection among invertebrates (Eberhard 1996; Arnqvist 1998; Hosken and Stockley 2004; Simmons et al. 2009), the relationship between genital morphology and postcopulatory sexual selection remains equivocal for vertebrates as comparative studies in mammals reveal contradictory evolutionary responses in genital morphology to variation in postcopulatory sexual selection (Dixson 1998; Hosken et al. 2001; Ferguson and Larivière 2004; Ramm 2007). Finally, using these data for pinnipeds, we directly test Parker et al.'s (2012) recent prediction of a negative relationship between expenditure on pre- and postcopulatory traits within a comparative framework.

Methods

DATA COLLECTION

Data on male and female body mass and male sexual traits were collected from the literature (see Supporting information for raw data and additional information). Body mass data were available for all extant pinnipeds, whereas data on testes mass and baculum (os penis) length (the most widely reported baculum characteristic) were available for 14 and 25, respectively, of the 33 extant species of pinnipeds. In contrast with the complex baculum morphology in other mammals (e.g., rodents and other carnivores, Burt 1960), the pinniped baculum exhibits a relatively simple morphology, consisting primarily of a straight or slightly curved structure (Miller 2008). However, despite the consistency in overall morphology, pinniped baculum length exhibits dramatic variation across species (Scheffer and Kenyon 1963). Data from the peak of the reproductive season were used whenever available. To account for geographic variation in body size and reproductive traits, we attempted to match the location where variables were measured as closely as possible. For 13 of the 14 species where testes mass was available, we found male and female body mass data from geographically similar study populations, whereas baculum length data were available from similar study populations for 12 of the 14 species where data on testes mass were available. In the few cases where we could not match data based on geography, we used mean body mass and baculum length values from the literature. For the remainder of species examined in this study, we collected body mass and baculum length from previously published reviews. SSD in body mass was calculated from male and female mass data using the formula log (male body mass/female body mass) (Fairbairn 2007). Body size and SSD were used as proxy measures of the strength of precopulatory sexual selection (Clutton-Brock et al. 1977; Alexander et al. 1979; Webster 1992; Dunn et al. 2001; Gonzalez-Voyer et al. 2008), whereas testes mass (corrected for body mass) was used as a proxy measure for the strength of postcopulatory sexual selection (Birkhead et al. 2009). We also investigated how baculum length relates to pre- and postcopulatory sexual selection by assessing the relationship between body size corrected baculum length and SSD and body size corrected testes mass.

SEXUAL SELECTION AND RATES OF PHENOTYPIC EVOLUTION

Traits that are subject to sexual selection typically exhibit faster rates of evolutionary divergence (Andersson 1994; Gonzalez-Voyer and Kolm 2011). Therefore, we asked whether the rate of phenotypic divergence in reproductive traits differed consistently based on the level of sexual selection experienced by a species. We investigated rates of phenotypic divergence in male and female body mass and SSD to gain insights into how selection operates on precopulatory traits. In a previous study, we examined rates of divergence in male and female body mass among pinnipeds (Fitzpatrick et al. 2012). However, the data used in our previous study differed slightly from that analyzed here, as the present study used different body mass measures in an effort to minimize geographic variation in trait values (see above). Therefore, we re-examined rates of phenotypic divergence in male and female body mass in this study. To investigate how selection operates on postcopulatory traits, we assessed rates of phenotypic divergence in body size corrected baculum length and testes mass extracted from phylogenetically controlled generalized least-squared regressions (see below for more details on these regressions). Pinnipeds were categorized into two groups—species with harems and without harems—based on mean harem size values collected from the literature (Lindenfors et al. 2002): species with harems consisted of those where males control territories with more than 1 female present ($n = 19$ species) and species without harems consist of those where males pair socially or serially with a single female ($n = 14$ species). After categorizing species into those with and without harems, we reconstructed the ancestral states of these groups using maximum-likelihood Mk1 models in Mesquite version 2.75 (Maddison and Maddison 2011) and assigned branches in the phylogeny as those with or without harems based on ancestral state reconstruction analyses (see the labeled phylogeny in the Supporting information). All phylogenetic analyses were performed using a molecular supertree of all extant pinnipeds kindly provided by Jeff Higdon (Higdon et al. 2007).

We then compared the rates of phenotypic divergence in body mass, SSD, and reproductive traits between the two groups using phenotypic diversification rate tests. All analyses were performed using the MOTMOT package (Thomas and Freckleton 2011) in R version 2.10.1 (R Foundation for Statistical Computing 2009). MOTMOT uses a maximum-likelihood method to assess the expected similarity between two variance–covariance matrices (in this case between species with and without harems). Then, to obtain a variance–covariance matrix expected from a Brownian model of trait evolution, MOTMOT applies a scalar parameter, θ, to one of the two matrices. In our analyses, we applied θ to the groups comprised of species with harems. The maximum-likelihood value of θ was estimated, where deviations from $\theta = 1$ are indicative of differences in the rate of trait evolution between the groups (Thomas et al. 2009). To clearly display the results, the θ parameter was rescaled such that $\theta = 1$ for the species without harems group. Thus, for the species with harems group θ values greater than one indicate comparatively rapid rates of phenotypic diversification while θ values less than one indicate comparatively slower rates of trait diversification. The 95% confidence intervals (CIs) for θ values were calculated based on the maximum-likelihood models. For each trait, we compared the maximum likelihood of the model against a model assuming equal rates of diversification using a likelihood ratio statistic that was estimated with chi-squared distribution and one degree of freedom. In all models, we assumed that each group had a different phylogenetic mean (Thomas et al. 2009). However, when performing the analyses assuming a common phylogenetic mean we found qualitatively similar results (data not shown).

PHYLOGENETICALLY CONTROLLED MULTIPLE REGRESSIONS

Phylogenetically controlled generalized least-squared (PGLS) regression analyses were used to account for nonindependence of data due to shared ancestry (Freckleton et al. 2002). All analyses were performed using log-transformed data in the APE package of the statistical program R version 2.10.1 (R Foundation for Statistical Computing 2009). PGLS regressions use maximum-likelihood methods to estimate a phylogenetic scaling parameter, λ, which evaluates the phylogenetic relationships of the covariance in the residuals in the model. Likelihood ratio tests were used to assess if λ values differed significantly from 0 or 1, where $\lambda = 0$ denotes no phylogenetic dependence and $\lambda = 1$ denotes strong phylogenetic dependence (Pagel 1999; Freckleton et al. 2002). For all analyses, Higdon et al.'s (2007) molecular supertree with branch lengths included was used to account for the phylogenetic relationship among pinniped species.

The relationships between reproductive traits and the degree of sexual selection were assessed using separate PGLS regressions with body mass added as a covariate in all analyses to account for allometric effects (García-Berthou 2001; Freckleton 2002). The relationship between baculum length and postcopulatory sexual selection was first assessed by adding testes mass and body mass as independent variables in the model, thus providing a measure of residual testes mass which is frequently used as a proxy for the postcopulatory risk of sperm competition (Gage and Freckleton 2003). The relationships between baculum length and testes mass and sexual selection were then assessed using SSD as an independent proxy for the strength of precopulatory sexual selection, as previous studies have demonstrated that high levels of SSD are associated with highly polygamous mating systems where the strength of precopulatory male–male competition is elevated (e.g., Clutton-Brock et al. 1977; Alexander et al. 1979; Webster 1992; Dunn et al. 2001; Gonzalez-Voyer et al. 2008). To account for the use of the same variable in multiple models, while avoiding the increased probability of committing type II errors associated with Bonferroni corrections, we calculated effect sizes, *r*, to assess the relationship between dependent and predictor variables and their 95% CI from *t* values obtained in PGLS regressions (Nakagawa 2004; Nakagawa and Cuthill 2007).

Results

Analyses of rates of phenotypic evolution revealed that almost all of the traits assessed in this study evolved faster in species with harems, consistent with previous studies showing that they experience relatively higher levels of sexual selection (see Introduction). Specifically, the maximum-likelihood estimate of θ was significantly greater for male ($\chi^2 = 9.86$, $P = 0.002$) and female ($\chi^2 = 7.79$, $P = 0.005$) body mass, SSD ($\chi^2 = 10.84$, $P = 0.001$), and body size corrected residual baculum length ($\chi^2 = 5.77$, $P = 0.02$) in the species with harems than in species without harems (Fig. 1). In contrast, residual testes mass was the

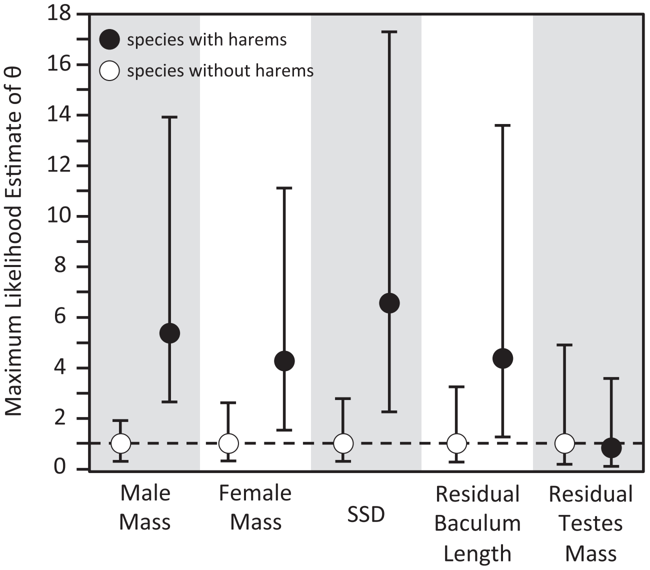

Figure 1. Rates of phenotypic evolution of body mass and sexual traits in pinnipeds. The maximum-likelihood estimates of the relative rate of phenotypic diversification (θ) and their 95% confidence intervals are shown for male and female body mass, sexual size dimorphism (SSD), body size corrected residual baculum length, and residual testes mass. Each trait is grouped into species with (filled circle) and without (open circle) harems. The dashed line shows $\theta = 1$ values. For all models, the θ value were rescaled so that the species without harems group had $\theta = 1$.

Table 1. **Multiple regressions models of baculum length and testes mass in relation to body mass and various predictor variables when controlling for phylogenetic effects using PGLS. The superscripts after the phylogenetic scaling parameter λ indicate if the λ value was significantly different than 0 (first position) and 1 (second position) in likelihood ratio tests. Nonsignificant values are indicated with "ns" and significant ($P < 0.05$) values are indicated by "∗". Significant relationships are presented in bold text. Effect sizes, *r*, and noncentral 95% confidence intervals (CIs) were calculated for each multiple regression.**

Trait	λ	Predictor	Slope ± SE	*t*	*P*	*r*	df	CI
Baculum length	$<0.001^{ns,ns}$	Testes mass	0.36 ± 0.11	**3.25**	**0.01**	**0.70**	**11**	**0.24–0.86**
		Body mass	0.15 ± 0.11	1.37	0.20	0.38	11	−0.21 to 0.71
Baculum length	$1.0^{*,ns}$	SSD	−0.29 ± 0.10	**−2.88**	**0.01**	**−0.53**	**21**	**−0.15 to 0.74**
		Body mass	0.37 ± 0.05	**7.39**	**<0.001**	**0.85**	**21**	**0.69–0.91**
Testes mass	$1.0^{ns,ns}$	SSD	−0.01 ± 0.48	−0.01	0.99	−0.003	11	−0.51 to 0.51
		Body mass	0.75 ± 0.15	**5.14**	**<0.001**	**0.84**	**11**	**0.55–0.92**
Testes mass	$<0.001^{ns,ns}$	SSD	−1.13 ± 0.27	**−4.22**	**0.002**	**−0.80**	**10**	**−0.43 to 0.91**
(*Callorhinus ursinus* removed)		Body mass	0.84 ± 0.13	**6.61**	**<0.001**	**0.90**	**10**	**0.70–0.95**

only trait examined where the rate of phenotypic evolution did not differ between species with and without harems ($\chi^2 = 0.04$, $P = 0.83$, Fig. 1). We obtained qualitatively similar results when we did not account for the effects of body mass and instead assessed absolute baculum length and testes mass (baculum length: $\chi^2 = 10.04$, $P = 0.002$; testes mass: $\chi^2 = 2.21$, $P = 0.14$). There was a nonsignificant statistical trend toward greater body size corrected baculum length in species without harems than in species with harems (harem group: $t = -1.80$, $P = 0.09$; body mass: $t = 6.33$, $P < 0.001$), whereas testes mass did not differ between species with and without harems (harem group: $t = -0.36$, $P = 0.73$; body mass: $t = 4.73$, $P = 0.001$).

Baculum length was positively associated with relative testes mass, a proxy measure of sperm competition risk (Table 1; Fig. 2A), suggesting that postcopulatory sexual selection promotes the evolution of longer bacula in pinnipeds. However, an assessment of how baculum length and testes mass were related with SSD, a proxy for precopulatory sexual selection, revealed a different pattern. Body size corrected baculum length was smaller in species with more extreme SSD (Table 1; Fig. 2B). There was no relationship between body size corrected testes mass and the degree of SSD when assessing all species where data were available (Table 1). However, when Northern fur seals, *Callorhinus ursinus*, a species with particularly large testes for their level of SSD, were removed from the analysis there was a negative relationship between testes mass and SSD after accounting for body size (Table 1; Fig. 2C). Removing the walrus, *Odobenus rosmarus*, which has the largest known baculum (Dixson 1995) and is an outlier in Fig. 2A, B, from the analyses did not alter the results: when controlling for body size, baculum length remained significantly positively related with testes mass ($n = 13$, testes mass: $t = 2.87$, $P = 0.02$; body mass: $t = 0.12$, $P = 0.26$) and negatively related with SSD ($n = 23$, SSD: $t = -3.73$, $P = 0.001$; body mass: $t = 8.37$, $P < 0.001$).

Finally, we assessed whether the pattern of negative covariance in baculum length and testes mass with SSD differed between species with and without harems. Although the sample sizes are inevitably reduced following this kind of partitioning of the data, we include these additional analyses as they directly address Parker et al.'s (2012) predictions regarding the relationship between pre- and postcopulatory traits in species groups experiencing different levels of male contest competition. In species without harems, there was no association between baculum length or testes mass and SSD in multiple regressions that controlled for body mass (baculum length: $n = 10$, SSD: $t = -0.22$, $P = 0.83$; body mass: $t = 2.66$, $P = 0.03$; testes mass: $n = 5$, SSD: $t = 0.03$, $P = 0.98$; body mass: $t = 1.07$, $P = 0.40$). In contrast, in species with harems the association between body size corrected baculum length and SSD remained significantly negative ($n = 14$, SSD: $t = -2.46$, $P = 0.03$; body mass: $t = 6.69$, $P < 0.001$). Similarly, when *C. ursinus* was removed from the analysis (as above), body size corrected testes mass was also negatively associated with SSD in species with harems ($n = 8$, SSD: $t = -2.84$, $P = 0.04$; body mass: $t = 6.86$, $P = 0.001$).

Discussion

Our results suggest that sexual selection drives rapid evolutionary divergence in traits that offer fitness advantages during pre- and postcopulatory episodes of sexual selection in pinnipeds. Phenotypic divergence in body mass and SSD was greater in species with harems, which is consistent with previous studies in pinnipeds (Lindenfors et al. 2002; Fitzpatrick et al. 2012). Rapid evolutionary divergence in male mass, and consequently SSD, is easily explained given the clear fitness benefits of increases in male body mass in pinniped species where precopulatory male–male competition is intense (see Introduction). However, the selective pressures promoting an increased divergence in

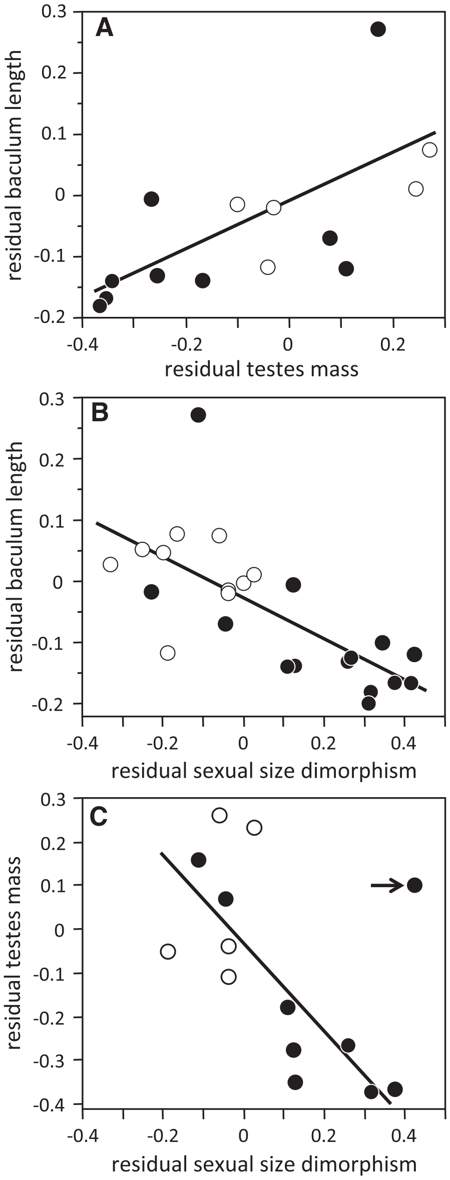

Figure 2. Partial correlation plots (after controlling for male body mass) depicting the relationship between (A) residual baculum length on residual testes mass, (B) residual baculum length, and (C) residual testes mass on residual sexual size dimorphism (SSD). Residual values were calculated from phylogenetically controlled generalized least-squared regressions and used in plots for clarity of presentation. All analyses were performed on phylogenetically controlled data using multiple regressions (see Methods and Table 1). Open circles indicate species without harems whereas filled circles indicate species with harems. In (C), the relationship between residual testes mass and residual SSD became significant after the removal of *Callorhinus ursinus* (indicated with arrow). All data are available in the Supporting information.

female body mass are less clear. Previously, we argued that the rapid divergence in female body mass in species with harems may be driven by genetic correlations in body size between the sexes (Fitzpatrick et al. 2012), although this hypothesis remains speculative. Sexual selection also influences the rate of genital evolution in pinnipeds, as phenotypic divergence in baculum length was faster in species where males control harems than in species where males are incapable of holding harems. This result is consistent with those of previous comparative and experimental evolution studies that demonstrate rapid evolution of genital shape in response to sexual selection in insects (Arnqvist 1998; Simmons et al. 2009; Rowe and Arnqvist 2011). However, to our knowledge this is the first such demonstration of rapid phenotypic divergence in genital size in response to sexual selection in vertebrates. Given the well-characterized coevolutionary responses in male and female genital morphology (Arnqvist and Rowe 2002; Brennan et al. 2007; Evans et al. 2011; Simmons and García-González 2011), we suggest that phenotypic divergence in baculum length may have been driven by the rapid divergence in female body size in response to sexual selection, assuming this generates concomitant changes in female reproductive tract dimensions.

Divergence in testes mass was the only phenotypic trait examined that did not differ between species with and without harems. Although we cannot discount the possibility that the reduced amount of data available for testes mass in pinnipeds limited our ability to detect differences between these groups, we put forward two possible explanations for this result. First, selection on testes size may be relaxed in pinnipeds. In harem-holding species, where SSD and variance in male mating success is extreme, a small number of territorial males secure the majority of reproductive success (Le Boeuf 1974; Le Boeuf and Reiter 1988; Fabiani et al. 2004; Kiyota et al. 2008; Pörschmann et al. 2010). With such high reproductive skew, the risk of sperm competition may be low and therefore selection to increase testes size above the naturally selected testes size in species with harems would be relaxed or absent. Alternatively, sperm competition may occur in pinnipeds but it either occurs with equal frequency in species with or without harems or it is more common in species with harems but these males lack the energetic resources to invest in producing larger testes. In pinniped species with harems, there is mounting evidence that males who are unable to physically dominate rivals engage in alternative mating tactics by attempting to surreptitiously copulate with females (Amos et al. 1993; Coltman et al. 1999; Hoelzel et al. 1999; Gemmell et al. 2001; Lidgard et al. 2004; Pörschmann et al. 2010). Although in other species, notably fishes (Montgomerie and Fitzpatrick 2009) and insects (Simmons 2001), such surreptitious matings increase the risk of sperm competition, whether this is the case in pinnipeds remains unclear. Therefore, it is difficult at present to distinguish between these two postcopulatory scenarios.

Nevertheless, our investigation of the relationships between traits that are subject to pre- and postcopulatory sexual selection suggests possible trade-offs or constraints in patterns of investment in pre- and postcopulatory sexually selected traits that underlie Parker et al.'s (2012) recent predictions, and are consistent with the idea that investment in testicular tissue may be limited in species where males invest resources into the control of harems. Body size corrected testes mass was negatively associated with SSD in pinnipeds overall, indicating a negative association between proxy measures for the strength of pre- and postcopulatory sexual selection. A closer examination of the relationship between pre- and postcopulatory sexual selection in species with and without harems revealed that the negative association between residual testes mass and SSD was strongest in species with harems. In their model, Parker et al. (2012) included a parameter, a, that described the mate-competition loading or the mating gain per unit expenditure on armaments. When $a > 1$, the gains from increased male precopulatory expenditure on weaponry exceeds the costs of that expenditure, as might be expected among harem mating systems. Parker et al.'s (2012) models predict that precopulatory expenditure should rise and postcopulatory expenditure decline with increased mate-competition loading, a. Our results suggest that in those pinniped species where males control harems, and precopulatory male–male competition is strongest, investment in postcopulatory traits is reduced as males invest greater resources in weaponry (i.e., body size). Although caution is required when assessing trade-offs among species, which may have different energy budgets (Parker et al. 2012), our results appear to provide phylogenetic comparative support for the predictions from Parker et al.'s (2012) contest-based sperm competition models, and suggest that a trade-off between pre- and postcopulatory expenditure by males might be greatest when the marginal gains from precopulatory expenditure are high.

However, the inherent limitations of comparative studies means that we are unable to assess if the negative relationship between pre- and postcopulatory traits is actually driven by trade-offs or simply because increased investment in precopulatory traits reduces the risk of sperm competition to the point where increased investment in postcopulatory traits becomes unnecessary. Although we lack the ability to evaluate either of these possibilities in detail, the presence of alternative mating tactics in pinnipeds (see above) suggests that postcopulatory traits may be important for securing paternity even in haremic species. Additionally, in some harem-holding pinnipeds and ungulates (e.g., Hoelzel et al. 1999; Preston et al. 2001) frequent mating by dominant males may lead to sperm limitation, which can reduce the harem-holding males' reproductive success. Thus, if sperm limitation is common in pinnipeds species where males control harems then this suggests that males who succeed in precopulatory contest competition by investing in large body size may suffer fitness costs by not being able to invest more in ejaculates. Therefore, we suggest that trade-offs between maximizing male competitive success during pre- and postcopulatory episodes of selection are a plausible explanation for the observed negative relationship between pre- and postcopulatory traits in pinnipeds.

Among the pinnipeds examined in this study, there was a positive relationship between body size corrected baculum length and testes mass. Such a positive relationship between baculum length and the strength of postcopulatory sexual selection is consistent with previous studies of carnivores (Ferguson and Larivière 2004; Ramm 2007), which report a positive relationship between baculum length and sperm competition risk. Similarly, initial investigations of genitalia among primates, which did not control for phylogenetic effects, suggested that female multiple mating was associated with longer bacula and more complex genital morphologies (Dixson 1987). Subsequent comparative studies of primates and bats that controlled for phylogenetic effects did not report a relationship between baculum length and the strength of postcopulatory sexual selection (Hosken et al. 2001; Ramm 2007). The negative relationship between baculum length and SSD in pinnipeds may be driven by the influence of sexual selection on the allometric relationship between baculum length and body size. Unlike in insects where genitalia typically exhibit negative allometry (Eberhard 2009), among mammals baculum length exhibits positive, isometric, and negative allometric relationships (Miller et al. 1998, 1999, 2000; Oosthuizen and Miller 2000; Miller and Burton 2001; Kinahan et al. 2008; Eberhard 2009; Schulte-Hostedde et al. 2011; Yurkowski et al. 2011). The variance in allometric relationship in genital size observed in mammals has recently been attributed to variance in the strength of pre- and postcopulatory sexual selection (Kinahan et al. 2008; Schulte-Hostedde et al. 2011). Specifically, genitalia are thought to exhibit positive allometry in species where postcopulatory sexual selection primarily influences fitness, whereas in species where males secure their reproductive success via precopulatory interactions genitalia are predicted to exhibit negative allometry (Kinahan et al. 2008; Schulte-Hostedde et al. 2011). Although not yet conclusive, there is some evidence supporting the hypothesis that mating systems influence genital allometry in mammals (Kinahan et al. 2008; Schulte-Hostedde et al. 2011; Yurkowski et al. 2011). Importantly for the present study, mating system appears to influence genital allometry in sexually mature pinnipeds, as genital allometry is typically isometric in species without harems (e.g., hooded seal, *Cystophora cristata*, Miller et al. 1999; ringed seal, *Pusa hispida*, Yurkowski et al. 2011), whereas genital allometry is negative in species where males control harems (e.g., stellar sea lion, *Eumetopias jubatus*, Miller et al. 2000; cape fur seal, *Arctocephalus p. pusillus*, Oosthuizen and Miller 2000). This contrasting pattern of genital allometry in response to mating system in pinnipeds may explain the negative relationship between male expenditure on precopulatory competition (SSD) and baculum size observed in this study.

In conclusion, we demonstrate that traits important in pre- and postcopulatory sexual selection exhibited faster rates of phenotypic divergence in species with harems than without harems and uncovered a positive relationship between two traits—residual baculum length and testes mass—that offer fitness advantages during postcopulatory male–male competition. Out of necessity, we focused on coarse measures of baculum length rather than shape, the latter of which has been argued to provide a clearer indication of how selection is operating on genitalia (Rowe and Arnqvist 2011). Thus, we foresee tremendous merit in gaining a more detailed understanding of how selection acts on genitalia in mammals by using the statistical tools of geometric morphometric analysis to characterize genital shape while assessing evolutionary questions in a phylogenetic framework (Rowe and Arnqvist 2011). We also show that investment in precopulatory traits that increase competitive ability in male–male contest competition is negatively associated with investment in postcopulatory traits among pinnipeds, as predicted by recent models (Parker et al. 2012). Future comparative tests of Parker et al.'s (2012) models in other systems that exhibit wide variance in the degree of investment in precopulatory weaponry, and a further investigation of how investment in precopulatory traits influences investment in additional postcopulatory traits, such as sperm morphology and velocity, would help to extend our understanding of the interaction between pre- and postcopulatory episodes of selection and assess if the patterns reported in this study are general or specific to pinnipeds.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Maximum-likelihood reconstruction of the degree of sexual selection in pinnipeds. Supporting Information may be found in the online version of this article.

Table S1. Species trait data for extant pinnipeds used in this study.

Supporting Information may be found in the online version of this article.