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No evidence for a trade-off between sperm length and male premating weaponry

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\textit{Running title:} Relationship between sexual traits

Abstract

Male ornaments and armaments that mediate success in mate acquisition and ejaculate traits influencing competitive fertilization success are under intense sexual selection. However, relative investment in these pre- and postcopulatory traits depends on the relative importance of either selection episode and on the energetic costs and fitness gains of investing in these traits. Theoretical and empirical work has improved our understanding of how precopulatory sexual traits and investments in sperm production covary in this context. It has recently also been suggested that male weapon size may trade off with sperm length as another postcopulatory sexual trait, but the theoretical framework for this suggestion remains unclear. We evaluated the relationship between precopulatory armaments and sperm length, previously reported in ungulates, in five taxa as well as meta-analytically. Within and between taxa, we found no evidence for a negative or positive relationship between sperm length and male traits that are important in male-male contest competition. It is important to consider pre- and postcopulatory sexual selection together to understand fitness, and to study investments in different reproductive traits jointly rather than separately. A trade-off between pre- and postcopulatory sexual traits may not manifest itself in sperm length but rather in sperm number or function. Particularly in large-bodied taxa such as ungulates, sperm number is more variable interspecifically and likely to be under more intense selection than sperm length. We discuss our and the previous results in this context.

Key words: male weaponry; male–male contest competition; meta-analysis; sexual selection; sexually selected traits; sperm competition; sperm length; trade-off.
Relationship between sexual traits

Introduction

Sexual selection is credited with driving the evolution of male armaments and ornaments (Darwin, 1871; Andersson, 1994), the size or elaboration of which typically influence male success in acquiring matings through male-male competition and/or female choice during precopulatory episodes of sexual selection (Andersson, 1994). However, females often mate with multiple males during the reproductive period (Jennions & Petrie, 2000; Hosken & Stockley, 2003; Arnqvist & Rowe, 2005). Consequently, sperm from different males can compete for fertilization (sperm competition; Parker, 1970) and females can bias the relative fertilization success of competing ejaculates in favor of preferred males (cryptic female choice; Thornhill, 1983; Eberhard, 1996). Ejaculate traits that enhance male fertility during competitive fertilizations will thus be favored by postcopulatory sexual selection and tend to evolve rapidly (Pitnick et al., 2009a). These ejaculate traits include sperm number and quality (e.g., sperm swimming speed, viability), both of which influence male competitive fertilization success (Snook, 2005; Simmons & Fitzpatrick, 2012; Fitzpatrick & Lüpold, 2014) and are shaped by variation in the strength of postcopulatory sexual selection (Møller, 1988; Harcourt, 1991; Parker & Pizzari, 2010; Gómez Montoto et al., 2011; Lüpold, 2013). However, although pre- and postcopulatory episodes of sexual selection are conceptually often treated as separate entities, both episodes of sexual selection can interact in influencing net male fitness (Kvarnemo & Simmons, 2013).

Since male armaments and ornaments influence male access to matings while ejaculate traits can affect the fertilization success following each mating, overall male reproductive success is determined by male investment in both sexual armaments/ornaments and ejaculates (Andersson & Simmons, 2006; Kvarnemo & Simmons, 2013). Whereas some males or species may be able to invest more in both pre- and postcopulatory sexual traits than others, which can result in positive covariation between different sexual traits despite resource trade-offs within males (van Noordwijk & de Jong, 1986), relative investment in pre- and postcopulatory sexual traits may
depend on the relative importance of either selection episode, as well as the energetic costs and fitness gains of investment in these traits. For example, due to the metabolic costs of both growing weapons used in precopulatory contest competition and investing in sperm production in response to sperm competition (Dewsbury, 1982; Olsson et al., 1997; Allen & Levinton, 2007; Emlen, 2008), the expression of sexually selected traits is likely to depend on the marginal benefits gained by increasing investment in either pre- or postcopulatory sexual traits (Parker et al., 2013). In taxa where males are rarely able to monopolize access to females, the importance of male–male competition both before and after mating might be of similar importance, meaning that selection should favor both pre- and postcopulatory sexual traits, thereby generating positive covariation between them (Parker et al., 2013). Conversely, if female monopolization is very common within a taxon, increased investment in precopulatory male–male competition at the cost of postcopulatory traits might yield greater fitness gains. In this scenario, the investment in postcopulatory sexual traits would decrease relative to that in precopulatory traits, either through energetic trade-offs in allocation to pre- and postcopulatory traits or because more intense female monopolization would increasingly limit the opportunity for sperm competition (and thus the value of investing in postcopulatory traits; Parker et al., 2013). Recently, empirical support for these predictions has emerged from a broad inter-taxonomic comparison (Lüpold et al., 2014) and comparative studies of marine mammals (pinnipeds: Fitzpatrick et al., 2012; cetaceans: Dines et al., 2015) that examined relationships between male investment in precopulatory armaments under selection through male–male contest competition and testes size, a trait capturing postcopulatory investments. As predicted by Parker et al.’s (2013) model, in taxa where males are not able to monopolize access to females, positive relationships between precopulatory armaments and testes size were detected, while in taxa where female monopolization is common, negative relationships between pre- and postcopulatory traits were observed (Fitzpatrick et al., 2012; Lüpold et al., 2014; Dines et al., 2015).
While these studies have linked variation in mating systems, secondary sexual traits and overall investment in ejaculates as measured by testes size, less is known about variation in ejaculate quality traits in this framework. For example, a recent meta-analysis of intra-specific studies on a broad range of secondary sexual traits (mostly under selection through female choice) and various ejaculate-quality traits found no relationship between these pre- and postcopulatory sexual traits (Mautz et al., 2013). By contrast, Ferrandiz-Rovira et al. (2014) reported a negative association between the expression of horns or antlers (i.e., premating sexual traits under male-male contest competition; Clutton-Brock, 1982; Preston et al., 2003) and sperm length across ungulate species (Bovidae and Cervidae). The differences in the taxonomic levels and types of premating sexual traits between these two studies make it difficult to draw general conclusions about the strength or direction of a link between precopulatory sexual traits and ejaculate quality traits, such that further examination is warranted. In particular, it remains unclear whether Ferrandiz-Rovira et al.'s (2014) results show a pattern unique to ungulates or whether it can be generalized to other mammalian and non-mammalian taxa that have evolved elaborate male weaponry as an integral component of male–male contest competition. Such a broader context is important because the theoretical foundation for a link between male armaments and sperm size currently remains very unclear, and similarities or differences in such links in other taxa might highlight gaps in our current understanding of trait evolution and help us improve available theoretical models as necessary.

Parker et al.’s (2013) model argues that there must be fitness benefits of marginal increases in postcopulatory investment to influence precopulatory investment patterns. Yet, contrary to the available evidence for sperm number and apart from a few exceptions, sperm length itself typically does not influence competitive male fertilization success (reviewed in Simmons & Fitzpatrick, 2012). Moreover, following the traditional view that long sperm evolve in response to postcopulatory sexual selection due to their increased performance and associated competitive advantage (reviewed in Snook, 2005; Simmons & Fitzpatrick, 2012; Fitzpatrick & Lüpold, 2014),
sperm length would be predicted to show similar relationships with premating sexual traits as does relative testes size. Thus, within the context of Parker et al.’s (2013) model, one would predict that sperm length should covary positively with weapon size in taxa where female monopolization is rare, but negatively in those with widespread female monopolization due to decreasing importance of postcopulatory relative to precopulatory sexual selection. Yet, across ungulates the size of male armaments does not covary with testes size (Ferrandiz-Rovira et al., 2014; Lüpold et al., 2014) and sperm length is not correlated with relative testes size (Gomendio et al., 2011). Additionally, the propensity of female monopolization is moderate (Lüpold et al., 2014), and whether or not males defend harems or territories (i.e., presence or absence of female monopolization) does not appear to affect any of these male reproductive traits (Ferrandiz-Rovira et al., 2014). Consequently, although a relationship between male weaponry and sperm length may seem counterintuitive, it may create an opportunity to further our understanding of the macroevolutionary links between sperm, testes, premating sexual traits and variation in the mating system from a different perspective, particularly if the reported pattern holds also in other taxa.

Here, we evaluated the relationship between precopulatory armaments and sperm length for five taxa, including mammals (primates, ungulates), birds (pheasants and allies), and insects (stalk-eyed flies, dung beetles), for which sexually selected traits are well characterized (summarized in Lüpold et al., 2014). We then investigated the generality of all these intra-taxonomic results in meta-analyses. All five taxa with available data fall between 0 and 50% of species with female monopolization and so show a positive or no association between premating sexual traits and testes mass (Lüpold et al., 2014). Thus, within Parker et al.’s (2013) model and prevailing views of selection on sperm morphology (see above), we predicted that if sperm length is associated with male armament size, the direction of this relationship should be determined by the correlation between sperm length and relative testes mass (e.g., if sperm length increases with relative testes mass, it should also increase with male weaponry because relative testes mass
increases with male weapon size). In this framework, the ungulates might be close enough to the switch point (i.e., around 47% of species with female monopolization) to show a weakly negative association between sperm length and armaments. However, this relationship needs to be confirmed using a more rigorous analytical approach that examines the correlation between the pre- and postcopulatory sexual traits without an underlying assumption about causality because it is not clear a priori which trait would influence the evolution of the other.

Our intra-taxonomic analyses and a flexible meta-analytical approach revealed that overall, male weaponry and sperm length do not covary significantly at the macroevolutionary level. These findings do not support the suggested negative relationship in ungulates as the basis for a general trend across taxa.

**Materials and Methods**

*Data collection and study taxa*

We compiled species-specific mean values from the literature for male premating weaponry, male and female body size, testes size, and total sperm length (Tables S1–S5; deposited on Dryad, doi: 10.5061/dryad.g9049). Of the nine taxa of our previous study (Lüpold et al., 2014), in which we provided data on weapon, body and testes sizes, we were able to obtain data on sperm length for five taxa, including primates and ungulates (Tourmente et al., 2011; Ferrandiz-Rovira et al., 2014), pheasants and allies (Immler et al., 2007), stalk-eyed flies (Presgraves et al., 1999), and dung beetles (Simmons & Fitzpatrick submitted).

Sexual size dimorphism (SSD = male size / female size; Fairbairn, 2007) was calculated using body mass in primates, ungulates and pheasants and allies, while SSD was based on body length in stalk-eyed flies (Presgraves et al., 1999). SSD was not considered in dung beetles as female body size data was not available for any of the species for which we had measures of weapons, testes and sperm length. To avoid using ratios in our analyses, we calculated SSD as ln(male size) – ln(female size). Male- or female-biased SSD can evolve due to (a) sexual
selection on male size (Andersson & Norberg, 1981; Clutton-Brock et al., 1985; Székely et al., 2000; Lindenfors, 2002; Lindenfors et al., 2002), (b) selection for female fecundity (Shine, 1979; Prenter et al., 1999), and/or (c) selection for inter-sexual niche partitioning (Selander, 1966; Shine, 1989; Thom et al., 2004). Of these factors, intra-sexual selection is well established to be the primary selective force driving the male-biased SSD in primates and ungulates (e.g., Lindenfors et al., 2007) as well as in the pheasants and allies (Lislevand et al., 2009). However, less information is available for SSD in our fourth taxon with data on SSD, the stalk-eyed flies. Although we cannot entirely reject the possibility that in this taxon some level of the variation in SSD can be attributed to fecundity selection in females, species mating in aggregations, where intra-sexual selection (e.g., female monopolization) is likely to be stronger, have been reported to be more sexually dimorphic than those with no mating in aggregations (Kotrba, 1996; Wilkinson & Dodson, 1997). To confirm that SSD is affected by this mating behavior, we compared the levels of SSD between species that mate in aggregations and those that do not, after controlling for female body size and phylogeny (see below). Based on laboratory observations of 10 species (Kotrba, 1996) and size data from the literature (Presgraves et al., 1999; Baker & Wilkinson, 2001), the SSD tended to be more male-biased in species where mating activity is correlated with aggregation behavior compared to species in which it is not (N = 10; aggregation: t = 2.38, P = 0.05; female body length: t = 2.01, P = 0.08; λ = 0.87^{0.08, 0.37}). These results suggest that SSD in stalk-eyed flies is explained at least in part by sexual selection and thus also provides a valid proxy of premating sexual selection in this taxon, particularly in combination with our parallel analyses of male weaponry.

**Statistical analyses**

We conducted all analyses using the statistical package R version 3.1.1 (R Core Team 2014) and transformed all non-normal data distributions by logarithmic transformations in order to meet the parametric requirements of the statistical models. To account for statistical non-independence of
data points by shared ancestry of species, we conducted phylogenetic generalized least-squared (PGLS) regressions (Harvey & Pagel, 1991; Freckleton et al., 2002), based on the same molecular phylogenies as in our previous study (Lüpold et al., 2014; Supplementary Figures S1–S5). These PGLS models estimate the phylogenetic scaling parameter $\lambda$ to evaluate the phylogenetic relationship of the covariance in the residuals (Freckleton et al., 2002). We used likelihood ratio tests to establish whether the models with the maximum-likelihood value of $\lambda$ differed from models with values of $\lambda$ set to 0 or 1, respectively. Values of $\lambda$ close to 0 indicate phylogenetic independence and $\lambda$ close to 1 suggests a strong phylogenetic signal in the association of the traits (Freckleton et al., 2002). Throughout this paper we present $\lambda$ values with their associated $P$-values of the above likelihood ratio tests in superscripts (first against $\lambda = 0$, second against $\lambda = 1$). Although branch lengths were known for the primate and ungulate phylogenies, we assigned equal branch lengths to all phylogenies for consistency. The use of branch lengths did not change the conclusion of the results.

PGLS models were used to assess the relationship between sperm length and relative (body-size corrected) testes mass and to examine the size-controlled relationship between sperm length and the expression of traits under precopulatory sexual selection (sexual size dimorphism, length of canines, size of horns and antlers, tarsal spur length or the span of eye stalks). For the latter models, we used two different approaches. For consistency with previous studies (e.g., Ferrandiz-Rovira et al., 2014), we first conducted a phylogenetic multiple regression as described above, using either weapon size or sperm length as the response variable and the other trait as the predictor, with body size as a covariate in either case to account for allometric effects (García-Berthou, 2001; Freckleton, 2002). Such regression models calculate the standard error for the slope, and thus the test statistic, based on the fitted correlation structure of the residual error (which changes when response and predictor variables are reversed; see Results) and assume the predictor explains the variation in the response variable (i.e., being causative). However, both of these assumptions seem arbitrary in the case of the relationship between sperm length and
premating sexual traits (see above) as these models imply that postcopulatory sexual selection predicts the intensity of premating sexual selection. While this may be possible based on a recent model on the origin of premating (Darwinian) sexual selection (Parker, 2014), it would intuitively seem just as plausible that the variation in premating traits is associated with the extent of premating sexual selection, and that this sets the boundaries for postcopulatory sexual selection through the propensity of males monopolizing access to females (and so predicts selection on sperm length). Consequently, there is no clear *a priori* prediction of which variable should be considered as the response variable in the analysis on pre- and postmating sexual traits, so we re-analyzed this relationship using a phylogenetic partial correlation approach. To do so, we calculated the phylogenetically independent contrasts for the three variables of the multiple regression models, using the *pic* function in the R package *ape* (Paradis et al., 2004), and then calculated the pairwise correlation coefficients among the three variables using the standard equation (Crawley, 2007)

\[
r_{xy} = \frac{\sum xy}{\sqrt{\sum x^2 \sum y^2}} ,
\]

where *x* and *y* are the independent contrasts of two of the three variables. Using these correlation coefficients for each pair of traits, we subsequently calculated the partial correlation coefficient \( r_{xy,z} \) between variables *x* and *y* (e.g., variables of interest) while controlling for *z* (e.g., body size), using the equation (Crawley, 2007)

\[
r_{xy,z} = \frac{r_{xy} - r_{xz}r_{yz}}{\sqrt{(1-r_{xz}^2)(1-r_{yz}^2)}} .
\]

This partial correlation coefficient was then used to calculate the *t*-statistic (with degrees of freedom being \( N - 3 \)) and *P*-value as well as the 95% non-central confidence interval around \( r_{xy,z} \) (Nakagawa & Cuthill, 2007).

Low statistical power prevented a rigorous test of whether the intra-taxonomic relationships between precopulatory armaments and sperm length were directly linked to variation in the propensity of female monopolization among taxa (Lüpold et al., 2014). Instead, we used a
flexible meta-analytical method based on a linear mixed-effects model (REML), with each taxon grouped in the random factor, $r$ values as the dependent variable, and weighting by the inverse variance of the respective effect size statistic (Nakagawa et al., 2007). We further examined the total heterogeneity of a sample, $Q_{\text{REML}}$, which we tested against a $\chi^2$-distribution with the degrees of freedom being one smaller than the number of $r$ values in the model. A significant $Q_{\text{REML}}$ value indicates a greater variance among effect sizes than expected by chance (i.e., some explanatory variables may contribute to significant heterogeneity; Nakagawa et al., 2007).

Results

Sperm length and premating sexual traits

First, we examined for each of the five taxa the phylogenetically corrected relationships between sperm length and relative testes size as a proxy of sperm competition (Harcourt et al., 1981; Birkhead & Möller, 1998; Soulsbury, 2010; Simmons & Fitzpatrick, 2012). Holding body size constant, sperm length covaried negatively with testes mass in the pheasants and allies ($N = 24$ species; testes mass: $r = -0.41$, $P = 0.05$; body mass: $r = -0.18$, $P = 0.15$; $\lambda = 0.84^{<0.001,0.03}$), but was not significantly associated in the other four taxa ($|r| \leq 0.20$, $P \geq 0.26$; Supplementary Table S6).

We then examined the size-controlled relationships between sperm length and the expression of traits under premating sexual selection, using the latter as the predictor and sperm length as the response variable. As premating traits we used either the size of taxon-specific armaments or sexual size dimorphism (SSD), a proxy for the strength of premating sexual selection (e.g., Clutton-Brock et al., 1977; Webster, 1992). Phylogenetic multiple regressions controlled for body size did not reveal any significant associations between either weapon size and sperm length or SSD and sperm length in any of the taxa studied (all $|r| \leq 0.39$ and $P \geq 0.07$; Supplementary Tables S7 and S8). For direct comparison with Ferrandiz-Rovira et al.'s (2014) results, however, we also performed phylogenetic multiple regressions with sperm length as the
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predictor and premating sexual traits as response variables. Consistent with Ferrandiz-Rovira et al.’s (2014) analysis across 49 ungulate species, we found a borderline significant negative relationship between male weapon size and sperm length across all 64 species in our dataset (sperm length: \( r = -0.25, P = 0.05 \); body mass: \( r = 0.84, P < 0.0001 \); \( \lambda = 1.0^{-0.001}, 1.0 \); Supplementary Table S9). None of the other taxa, however, exhibited a significant relationship regardless of the premating sexual trait used (all \(|r| \leq 0.38 \) and \( P \geq 0.24 \); Supplementary Tables S9 and S10).

As there is no clear a priori prediction of which variable should be considered as the response variable when examining pre- and postmating sexual traits, we tested the same relationships again, but this time using a phylogenetically controlled multiple correlation approach, which removes this issue (for details see Materials and Methods). Controlling for phylogeny and body mass, these analyses again yielded no significant relationship between sperm length and premating sexual traits (weapons or SSD) in any of the examined taxa (Table 1).

Although none of the intra-taxonomic results were statistically significant, all relationships except for the ungulates exhibited a positive sign (Supplementary Tables S7 – S10). We thus performed a meta-analysis using a mixed-model approach (Nakagawa et al., 2007) based on the partial correlation coefficients from the above intra-taxonomic analyses to examine whether there was a positive overall association between the size of sperm and premating sexually selected traits. We found no significant overall effect with weapon size (\( Z_r = 0.02, t = 0.36, P = 0.74 \)) or SSD (\( Z_r = 0.16, t = 2.04, P = 0.11 \)) as the premating trait. For both meta-analyses we found no evidence for greater variance among effect sizes than expected by chance (both \( Q_{REML}: P > 0.98 \); also see Supplementary Tables S7 – S10).

Discussion

Within and across the five taxa examined, we found no significant relationship between sperm length and the size of external male weaponry or sexual size dimorphism as premating sexual
traits. The ungulates formed the only taxon with the potential for a significant association and the only taxon with a negative slope. All other taxa and the meta-analysis across all taxa showed no evidence for a relationship between sperm length and traits under premating sexual selection.

Although statistically some of our findings were comparable to a recent study of ungulates (Ferrandiz-Rovira et al., 2014), which reported a marginally significant negative relationship between the size of sperm and male horns or antlers, overall our conclusions contrast with that study. First, the negative association between sperm and weapon length in the ungulates was borderline significant only if weapon length was the response variable, whereas it was far from significant when using a phylogenetic partial correlation approach that is not sensitive to which trait is used as the response variable (also see Supplementary information for reversed variables). Second, our inter-taxonomic meta-analysis also revealed no significant overall effect, questioning the validity of generalizing drawn from the ungulate data. This is furthermore, consistent with a recent meta-analysis documenting no support for a general link between sperm size and the expression of a broader range of secondary sexual traits (Mautz et al., 2013). Therefore, we suspect that the previously reported negative covariance between male weaponry and sperm length in ungulates (Ferrandiz-Rovira et al., 2014) may be the result of the statistical approach used rather than representing a general biological pattern.

How sperm morphology would be predicted to covary with the expression of traits that are important in premating contest competition generally remains unclear and currently lacks a coherent theoretical framework. First, the role of sperm length itself in determining competitive fertilization success is still poorly understood, with studies showing positive, negative and no effects of sperm length on fertilization success (reviewed in Simmons & Fitzpatrick, 2012). Some of this confusion may stem from the fact that studies competing sperm of different lengths against one another typically do not account for confounding sperm number effects, particularly in internal fertilizers (but see Lüpold et al., 2012). Second, compared to the overall investment in sperm production as expressed by relative testes size, sperm size per se may not experience a
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direct allocation trade-off with weapon size. Rather, the intensity of selection on sperm number is likely to outweigh that on sperm size, particularly in large species due to dilution effects, which may, past a certain threshold related to the spermatogenic capacity or metabolism of the testes (e.g., Lüpold et al., 2009b; Ramm & Stockley, 2010), result in a reduction in sperm length (Parker et al., 2010; Immler et al., 2011). If in all the vertebrate taxa examined in this study sperm number is indeed under stronger selection than sperm length (also see Tourmente et al., 2015; Lüpold & Fitzpatrick submitted), this may be one of the reasons for the lack of a clear pattern of covariation between sperm length and investment in premating weaponry. At least for the pheasants and allies, for which we previously reported a significant positive association between relative testes size and SSD (Lüpold et al., 2014), the negative relationship between sperm length and relative testes size would intuitively suggest a negative relationship between sperm length and male premating sexual traits. However, this is not what we found, which may be the result of limited statistical power or because the nature of such relationships is more complex. Predicting the association between investments in sperm length and premating sexual traits, respectively, may be even more difficult for the two mammalian taxa, in which sperm length appears to be independent of sperm competition levels (also see Gomendio et al., 2011; but see Anderson & Dixson, 2002 for positive covariation for sperm midpiece volume in primates).

It seems very plausible that the processes of selection are fundamentally different between sperm and male armaments, with any association between these traits not necessarily being causative. For example, characters under premating sexual selection tend to be complex somatic traits that are often under multi-genic control (e.g., Lande, 1980). These premating sexual traits tend to be highly condition-dependent and to visually signal their bearer's underlying condition to competitor males (e.g., to avoid potentially lethal physical combat among males of unequal condition) and, at least in some taxa, to females (reviewed in Emlen, 2008). By contrast, sperm traits are borne by single haploid cells, which, in internal fertilizers, operate within the selective
environment of the female reproductive tract. Consequently, unlike many traits under premating
sexual selection, for which variation in specific phenotypes often has direct fitness consequences,
selection on sperm traits is not independent of physical and biochemical sperm–female
interactions (Pitnick et al., 2009a; b). Such interactions may result in stabilizing selection for an
‘optimal’ sperm phenotype (Calhim et al., 2007; Immler et al., 2008; Kleven et al., 2008; Lüpold
et al., 2009a; Fitzpatrick & Baer, 2011; Varea-Sánchez et al., 2014), and, at the
macroevolutionary scale, in coevolution between sperm length and critical components of the
female reproductive tract (Briskie et al., 1997; Presgraves et al., 1999; Miller & Pitnick, 2002;
Anderson et al., 2006; Higginson et al., 2012). Furthermore, selection may often primarily target
sperm function (e.g., sperm velocity, longevity, surface proteins) rather than sperm gross
morphology per se, with sperm dimensions changing secondarily in response to such selection
because they mediate sperm function. For example, in externally fertilizing cichlid fishes
improved sperm swimming speed and energetics appear to have preceded the evolution of longer
sperm (Fitzpatrick et al., 2009). Finally, in contrast to the typically condition-dependent variation
in male armaments (Emlen, 2008) and many other axes of ejaculate quality (reviewed in Pitnick
et al., 2009a; Simmons & Fitzpatrick, 2012; Fitzpatrick & Lüpold, 2014), the morphology of
sperm appears to be highly heritable and much less dependent on male condition (reviewed in
Pitnick et al., 2009a; Simmons & Moore, 2009; but see Simmons & Kotiaho, 2002). Even in taxa
such as Drosophila, in which sperm are relatively long and costly (Pitnick, 1996) and sperm size
is well established to be under particularly intense sexual selection (Bjork & Pitnick, 2006;
Immler et al., 2011; Lüpold et al., 2012), sperm size is not condition-dependent. Rather, sperm
number becomes increasingly condition-dependent as the investment per sperm increases across
species (i.e., only high-quality males can invest in more sperm given the elevated costs per sperm
cell; Lüpold et al., in prep.). In this context, differential resource allocation between secondary
sexual traits and ejaculates may be more likely to involve other ejaculate traits than sperm length
itself.
In conclusion, in contrast to a recent study of ungulates (Ferrandiz-Rovira et al., 2014), neither our results nor those of a meta-analysis on a broader range of sexually selected traits (Mautz et al., 2013) provide support for a negative relationship between sperm length and the expression of premating sexual traits. Thus, an allocation trade-off between pre- and postcopulatory sexual traits may be more likely to manifest itself in testes size and sperm number or function than in sperm length, with sperm number likely to be under more intense selection than sperm length in most taxa.

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References

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Table 1: Phylogenetically controlled partial correlations between (a) weapon size and sperm length and (b) SSD and sperm length, controlled for body size. The partial correlation coefficients $r_{xy.z}$ are presented with their lower (LCL) and upper (UCL) non-central 95% confidence limits.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Partial $r_{xy.z}$ (LCL, UCL)</th>
<th>df</th>
<th>$t$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Precopulatory weapons</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primates (canine height)</td>
<td>0.18 (–0.18, 0.48)</td>
<td>30</td>
<td>1.00</td>
<td>0.33</td>
</tr>
<tr>
<td>Ungulates (horn/antler length)</td>
<td>–0.19 (–0.41, 0.06)</td>
<td>61</td>
<td>–1.52</td>
<td>0.13</td>
</tr>
<tr>
<td>Pheasants and allies (spur length)</td>
<td>0.01 (–0.20, 0.42)</td>
<td>19</td>
<td>0.06</td>
<td>0.96</td>
</tr>
<tr>
<td>Dung beetles (horn length)</td>
<td>0.10 (–0.39, 0.53)</td>
<td>14</td>
<td>0.37</td>
<td>0.72</td>
</tr>
<tr>
<td>Stalk-eyed flies (eye span)</td>
<td>0.01 (–0.54, 0.55)</td>
<td>9</td>
<td>0.02</td>
<td>0.98</td>
</tr>
<tr>
<td>(b) Sexual size dimorphism</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primates</td>
<td>0.16 (–0.16, 0.44)</td>
<td>37</td>
<td>0.97</td>
<td>0.34</td>
</tr>
<tr>
<td>Ungulates</td>
<td>–0.01 (–0.25, 0.24)</td>
<td>60</td>
<td>–0.06</td>
<td>0.95</td>
</tr>
<tr>
<td>Pheasants and allies</td>
<td>0.22 (–0.29, 0.60)</td>
<td>14</td>
<td>0.85</td>
<td>0.41</td>
</tr>
<tr>
<td>Stalk-eyed flies</td>
<td>0.37 (–0.32, 0.74)</td>
<td>8</td>
<td>1.12</td>
<td>0.30</td>
</tr>
</tbody>
</table>