

REVIEW

Variance in male reproductive success and sexual size dimorphism in pinnipeds: testing an assumption of sexual selection theory

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Running title: Does sexual selection explain size dimorphism?

ABSTRACT

1. The theory of evolution by sexual selection for sexual size dimorphism (SSD) postulates that SSD primarily reflects the adaptation of males and females to their different reproductive roles. For example, competition among males for access to females increases male body size because larger males are better able to maintain dominant status than smaller males. Larger dominant males sire most offspring while smaller subordinate males are unsuccessful, leading to skew in reproductive success. Therefore, species with male-biased SSD are predicted to have greater variance in male reproductive success than those in which both sexes are similar in size.

2. We tested this prediction among the Pinnipedia, a mammalian group with great variation in SSD. From a literature review we identified genetic estimates of male reproductive success for 10 pinniped taxa (eight unique species and two subspecies of a ninth species) that range from seals with similarly sized males and females to species in which males are more than four times as large as females.
3. We found no support for a positive relationship between variance in reproductive success and SSD among pinnipeds after excluding the elephant seals *Mirounga leonina* and *Mirounga angustirostris*, which we discuss as distinctive cases.
4. Several explanations for these results are presented including the revival of one of Darwin's original ideas. Darwin proposed that natural selection may explain SSD based on differences in energetic requirements between sexes and the potential for sexual niche segregation. Males may develop larger bodies to exploit resources that remain unavailable to females due to the energetic constraints imposed on female mammals by gestation and lactation. The importance of this alternative explanation remains to be tested.

Keywords: bioenergetics, genetic paternity, habitat differentiation, mating behaviour, marine mammals.

INTRODUCTION

In most mammals, including humans, males are on average larger than females (Ruckstuhl & Neuhaus 2005). Most explanations of sexually related characters rely on sexual selection theory (Hedrick & Temeles 1989, Shine 1989, Isaac 2005). When females are conditioned to perform almost all parental investment, as is the case in mammals, males compete for access to mates and polygyny evolves as the most common type of mating system. The degree of polygyny depends firstly on the distribution of resources and secondly on the distribution of females (Emlen & Oring 1977). The theory of evolution by sexual selection for sexual size dimorphism (SSD) postulates that competition among males for access to females increases aggression and male body size, because larger males are better able to maintain a dominant status (Trivers & Willard 1973).

Until the 1980s, this hypothesis was apparently supported by empirical evidence, particularly from observations of strong associations between SSD and parental investment in offspring, and between SSD and the level of polygyny (Lindenfors et al. 2007). This was built on the assumption that genetic and behavioural levels of polygyny are correlated. This means that in a monogamous system, males should be parents of offspring born to their partners and, in a polygynous system, males should have a degree of paternity that is directly proportional to the number of females with which they are able to associate through success in competition with other males. Since the 1980s, advances in the use of molecular markers to estimate paternity have shown that in some cases these assumptions are not met: extra-pair copulations often occur in monogamous species, while in polygynous species, subordinate males often achieve more copulations than predicted by their social rank.

In this study, we evaluated the role of sexual selection in the evolution of SSD in pinnipeds (Pinnipedia), a group that shows the widest variation in SSD among higher vertebrates and has varying degrees of polygyny (Ralls & Mesnick 2002). Most true seals (Phocidae) and the walrus (Odobenidae) mate at sea or on ice, and exhibit slight to moderate polygyny, whereas eared seals

(Otariidae) and elephant seals (Phocidae) mate on land and are moderately to highly polygynous. SSD has been traditionally assumed to be caused by sexual selection in pinnipeds (Bartholomew 1970), but to our knowledge this assumption remains untested. Using data gathered from the literature we conducted an interspecific comparison to test the prediction that male-biased SSD is positively related with variance in male paternity (genetically determined), as expected if sexual selection is the main force causing SSD in pinnipeds.

METHODS

We conducted a literature search during October 2012 using the Web of Knowledge to locate genetic studies of paternity in pinniped species. We identified a total of 15 publications for 11 species of pinnipeds (out of the 33 species recognized by Berta & Churchill 2012). The authors of three of the studies did not provide an estimate of variance in male reproductive success (V_{rep}) or the necessary data to estimate variance (Worthington Wilmer et al. 1999, Lidgard et al. 2004, Kiyota et al. 2008). We tried to contact the authors of these publications, but the data were not available or the authors could not be reached. Therefore, our final dataset included estimates of V_{rep} from 12 studies representing nine species (Table 1). When multiple estimates of V_{rep} were available from one study (e.g. estimates derived from different methods or with different levels of confidence), we used the most conservative estimate or the method defined as preferable by the authors. Results (not shown) were not qualitatively different when we used alternative estimates. Body mass data were obtained from Lindenfors et al. (2002) and Fitzpatrick et al. (2012). We define SSD as the ratio of mean male adult body mass (g) to mean female adult body mass (g). This is a convenient index when one sex is always larger (Fairbairn 2007), as was the case in our dataset in which males are larger than females for all species. However, in some pinniped species females can be larger than males (Ralls & Mesnick 2002).

To explore the relationship between V_{rep} and SSD we used two different approaches. First, we fitted phylogenetic generalized least square (PGLS) models (Martins & Hansen 1997) that

correct for the lack of independence due to evolutionary relationships. These models require a single estimate per species, thus we calculated median variances for species with >1 estimate, and averaged data for *Phoca vitulina*. PGLS models were fitted by using the procedures ‘corpagel’ (ape package in R, Anonymous 2011) and ‘gls’ (nlme package in R). The phylogenetic relationships were defined by the best date estimates of the mammalian supertree (Fritz et al. 2009). The second analysis was based on taxonomically-corrected generalized linear mixed models (GLMM), and allowed us to use all data estimates. GLMMs included nested random effects of family, genus and species to control for non-independence of the data, and were fitted with the procedure ‘MCMCglmm’ in R using uninformative priors ($V=1$, $\nu=0.002$), 300000 iterations, thinning every 100 iterations, and a burn-in period of 30000.

In all models V_{rep} was defined as the variance in the number of pups sired per male over a variable time period (2-7 breeding seasons), and calculated to include all sampled males (successful and unsuccessful). To control for any effects of the length of the study we included duration (in years) as a fixed factor. Ideally V_{rep} should be calculated using lifetime reproductive success, but estimates of lifetime reproductive success are rare, particularly for long-lived species such as pinnipeds.

RESULTS

An extreme estimate for *Mirounga leonina* ($V_{rep}=64$; Table 1) was identified as an outlier in all analyses, and was removed from the dataset. A second estimate for *Mirounga leonina* was available so our results apply to this species to a certain extent.

The PGLS model shows that higher V_{rep} is significantly associated with greater SSD ($\beta=1.5$, $SE=0.31$, $P=0.003$) but not with the duration of study ($\beta=0.1$, $SE=0.36$, $P=0.77$). The positive association between SSD and V_{rep} is not significant if data from both *Mirounga* species are excluded (SSD: $\beta=0.2$, $SE=0.47$, $P=0.63$; duration of study: $\beta=0.2$, $SE=0.27$, $P=0.42$). GLMM results show that higher V_{rep} is significantly associated with greater SSD ($\beta=1.7$, 95%CI=1.1-2.2,

$P < 0.001$) and with duration of study ($\beta = 0.5$, 95% CI = 0.1-0.7, $P = 0.02$), but again the positive association between SSD and V_{rep} is not significant when data from *Mirounga* are excluded (SSD: $\beta = -0.1$, 95% CI = -2.2-1.3, $P = 0.82$; duration of study: $\beta = 0.5$, 95% CI = 0.2-0.8, $P < 0.001$).

DISCUSSION

We did not find strong support for a relationship between V_{rep} and SSD. Considering all available data, the relationship is significant, but the pattern is driven by estimates from *Mirounga* (elephant seals), which are extreme cases for both SSD and V_{rep} (Table 1). Elephant seals have a conspicuous, secondary sexual character: the proboscis that gives the species their name and probably evolved via sexual selection (Sanvito et al. 2007). A large proboscis requires a large body, so selection to increase proboscis size may have secondarily led to increases in male body size for *Mirounga*. Excluding *Mirounga* we find no clear relationship between SSD and V_{rep} in pinnipeds. We offer three possible explanations for this finding:

1. Methodological limitations

We may have failed to detect a relationship because of our small sample size. Unfortunately, we cannot easily address this limitation as it requires additional studies of paternity in pinnipeds. However, though limited, our sample is generally representative of the variation in SSD among pinnipeds, so we would expect to observe a trend with V_{rep} if both are correlated.

Methodological limitations of the paternity studies themselves may have led to incorrect estimates of reproductive success that affected our analyses. Genotyping errors are possible and can affect paternity estimates (Hoffman & Amos 2005). However, these errors underestimate reproductive skew in general, and we have no reason to believe that genotyping errors are more likely in studies of species with greater SSD, as would be necessary to mask an existing relationship. Incorrect V_{rep} estimates may also occur if genetic material is not obtained from a representative sample of adult males. For example, if only territorial males (that are presumably

successful) are sampled, and other adult males are not included, we would expect lower V_{rep} than if all males were represented. However, in this case there should also be high mean values in the number of pups sired, and few, if any, unsuccessful males. In most studies we used, the mean number of pups assigned to each male was low (<1.3 ; Table 1) and many of the sampled males were not assigned any pups, suggesting that sampling was not limited to successful males. Notable exceptions are the two studies on *Mirounga*, in which high average numbers of pups per male are reported, and in which primarily successful males were sampled. In these studies V_{rep} is also high, suggesting that *Mirounga* spp. may have a distinct mating system in which successful males produce high but very variable numbers of offspring.

Finally, an important limitation is the lack of data on lifetime V_{rep} . We controlled for duration of the study as a way to address this limitation and to show whether longer studies resulted in higher estimates of V_{rep} . However, duration of study and SSD were not significantly correlated (Pearson $\rho = -0.38$, $P = 0.18$), thus this bias should not have affected our results. In conclusion, while methodological limitations are likely to exist, we do not think they are sufficient to explain the observed lack of a relationship for most pinnipeds.

2. Alternative mating strategies.

A variety of alternative mating behaviours has been described for pinnipeds (Cox & Boeuf 1977, Campagna et al. 1988, Cassini & Vila 1990, Campagna et al. 1992, Gemmell et al. 2001, Fabiani et al. 2004). However, while alternative mating strategies could reduce V_{rep} , differences in success among strategies are still expected, because larger males should still sire more offspring to compensate for the costs of increased body mass. Future studies in which both genetic paternity and behaviour are examined are necessary to clarify the role of alternative mating strategies among pinnipeds.

3. Natural selection as the driver of SSD

Finally, it is possible that male-biased SSD is not caused primarily by sexual selection in these species (Isaac 2005). Darwin (1859) proposed that natural selection may play a role in SSD, based on an initial difference in parental investment that results in different energetic demands for males and females. Endothermy presents an important constraint on the increase in mammalian female body size, since the energetic demands of gestation and lactation are high (Bowyer 2004). In addition, females spend time with their young, which can prevent them from foraging or resting. By not bearing the costs of gestation and lactation, male mammals have more energy and time available to invest in thermoregulation, foraging and growing. In pinnipeds, as males become larger, their total energetic requirements increase but, at the same time, they are able to move faster and deal with lower ocean temperatures than females. Larger male pinnipeds become capable of using colder and richer ocean waters, hence generating a selective pressure to increase male body mass where such resources are available. For example, Le Boeuf et al. (2000) found that, in *Mirounga angustirostris*, the richest foraging areas were those furthest from the rookery, and only the largest males were capable of reaching these distant sites. Differential use of resources by the sexes has previously been interpreted as a consequence of size differences primarily caused by sexual selection (Bartholomew 1970), but our results show that sexual selection is unlikely to explain SSD in the pinniped species we studied. Instead, niche differentiation may be the main driver of observed SSD for these species.

Conclusion

Despite its limitations, our analysis highlights the need to question basic assumptions of the theory of sexual selection, such as the relationship between dominance and reproductive success, which are not sufficiently tested. We present an alternative explanation for the evolution of SSD via natural selection, which may also operate in terrestrial mammals (Isaac 2005). The role of natural selection needs to be tested, but there is evidence that pinniped species with greater SSD exhibit sexual niche segregation both in diet and space (Staniland 2005), as predicted by this hypothesis. In

fact, both natural and sexual selection may play a role in the evolution of SSD, affecting different species or acting synergistically (Isaac 2005). For example, sexual selection, possibly reinforced by natural selection, may have led to larger male elephant seals, while resource use and bioenergetics constrains may explain size differences in other pinniped species.

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Table 1. Data from studies of genetic paternity for several pinniped species and subspecies included in our analyses

Taxa	SSD	Duration	Mrep	Vrep	Psucc	Genetic paternity study
Otaridae						
<i>Arctocephalus forsteri</i>	3.281	3	1.20	1.89	0.55	(Caudron et al. 2009)
<i>Arctocephalus gazella</i>	3.444	3	0.18	0.18	0.16	(Gemmell et al. 2001)
<i>Arctocephalus gazella</i>	3.444	7	0.99	2.85	0.44	(Hoffman et al. 2003)
<i>Zalophus californianus</i>	3.019	3	0.18	0.20	0.15	(Flatz et al. 2012), Los Islotes Island
<i>Zalophus californianus</i>	3.019	4	0.38	0.58	0.31	(Flatz et al. 2012), San Jorge Island
<i>Zalophus wollebaeki</i>	2.564	2	0.20	0.31	0.15	(Poerschmann et al. 2010), 2006-07
<i>Zalophus wollebaeki</i>	2.564	2	0.33	0.47	0.23	(Poerschmann et al. 2010), 2007-08
Phocidae						
<i>Halichoerus grypus</i>	1.132	6	0.57	1.31	0.35	(Twiss et al. 2006)
<i>Halichoerus grypus</i>	1.132	4	0.41	0.59	0.30	(Amos et al. 1993)
<i>Leptonychotes weddellii</i>	1.007	4	0.70	1.40	0.89	(Harcourt et al. 2007)
<i>Mirounga angustirostris</i>	4.662	2	3.60	4.84	0.90	(Hoelzel et al. 1999)
<i>Mirounga leonina</i>	6.205	2	4.83	8.81	1.00	(Hoelzel et al. 1999)

<i>Mirounga leonina</i>	6.205	3	3.90	64.00*	0.54	(Fabiani et al. 2004)
<i>Phoca vitulina concolor</i>	1.140	3	0.02	0.00	0.02	(Coltman et al. 1998)
<i>Phoca vitulina richardsi</i>	1.352	4	0.07	0.07	0.07	(Hayes et al. 2006)

Estimates include: sexual size dimorphism (SSD), duration of the study (Duration, in years), the genetic estimate of average male reproductive success (Mrep, mean number of offspring sired by per male during the study period), variance in male reproductive success (Vrep), and proportion of sampled males assigned at least one paternity (Psucc). SSD was calculated as the ratio of mean adult male body mass (g) to mean adult female body mass (g), from mass data obtained from Lindenfors et al. (2002) and Fitzpatrick et al. (2012).

*value identified as an outlier in all analyses, and thus not used to define relationships