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Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds

Abstract Pinnipedia contains some of the most spectacular examples of sexual size dimorphism, examples that are therefore frequently used to illustrate the theory of sexual selection. This paper addresses the question of whether a significant relationship between sexual selection and size dimorphism exists in a comparative context. Thus, harem size and body size data gathered from the literature were analysed with independent contrasts analyses. These investigations showed that sexual size dimorphism is not a consequence of an allometric relationship between male and female size. Instead, there is a clear relationship between harem size and sexual size dimorphism. Further analyses also revealed a significant relationship between harem size and male size whereas no such relationship existed for females. These results support the hypothesis that sexual size dimorphism in pinnipeds is the product of an exclusively male response to sexual selection.

Introduction

Two of the most illustrative examples of Darwin's (1871) theory of sexual selection through male–male competition are the northern and southern elephant seals (*Mirounga angustirostris* and *M. leonina*). Intense and bloody male aggression, extremely skewed male mating success, and a resulting extraordinary size dimorphism

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provide convincing evidence of the powers of sexual selection.

In most pinnipeds females reach reproductive age much earlier than males, spending significant amounts of energy on their offspring and thus limiting their ability for further somatic growth. In contrast, males do not provide any parental care for the young and in most cases reach maturity later in life. They can therefore allocate more energy to growth and hence male pinnipeds often show a dramatic secondary growth spurt during their adolescent years. Although these differences in life histories of males and females are in accordance with sexual selection theory, the causal relationships may not be completely straightforward and sexual size dimorphism could in theory come about independent of sexual selection. A rigorous analysis of the selection pressures behind pinniped dimorphism needs to show that variation in sexual selection is correlated to varying levels of size dimorphism across the pinnipeds. A few such comparative studies have already been performed (e.g. Alexander et al. 1979; Weckerly 1998), particularly on otariids (e.g. Boness et al. 1991; Kovacs and Lavigne 1992). In none of these studies was phylogeny taken into account, however. The purpose of this paper is therefore to investigate the relationship between sexual selection and sexual size dimorphism in a phylogenetically correct manner.

In polygynous pinnipeds, males compete either for the control of harems or for access to areas where females aggregate (Haley et al. 1994; Pomeroy and Anderson 1994; Twiss and Pomeroy 1994; Trillmich 1996). Thus, physical characteristics giving advantages in male–male competition are selected for over time. One such important physical characteristic shown in earlier studies to be decisive in deciding the outcome in male conflicts over harems is body size (e.g. Anderson and Fedak 1985; Haley et al. 1994), which is what we investigate here.

Larger harems mean more intense sexual selection, which in turn means that the crucial character in competition becomes more important, i.e. more decisively

Fig. 1 The major axis regression lines through the origin (*thick lines*) on male and female **a** length contrasts and **b** weight contrasts. Neither slope is significantly different from a slope of 1.0 (*grey lines*) in that the 95% confidence intervals (*thin lines*) include a slope of 1.0. There is thus no significant relationship between body size and sexual size dimorphism
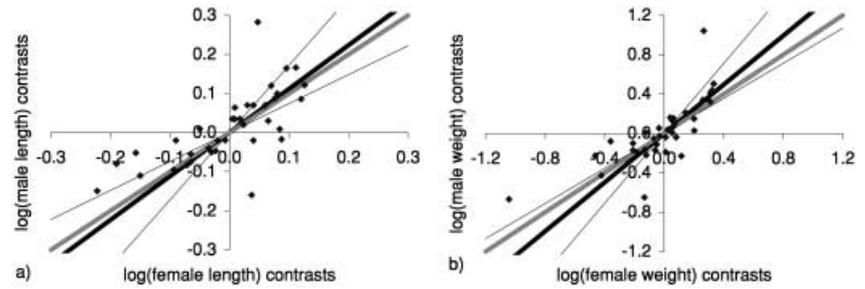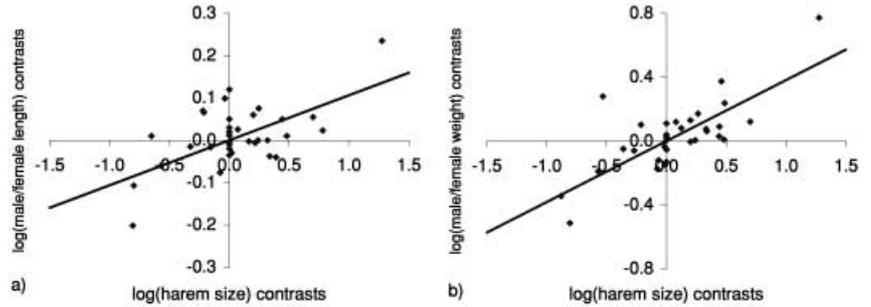

Fig. 2 The regression line through the origin on harem size and **a** length dimorphism contrasts and **b** weight dimorphism contrasts. There is a significant relationship between harem size and sexual size dimorphism

spread in the population. The hypothesis to be tested is consequentially straightforward: species in which average harem sizes are larger should be more sexually size dimorphic, not necessarily in absolute terms, but compared to their closest relatives with differing harem sizes.

Size dimorphism is a combined measure of the size of both sexes, whereas the theory of sexual selection in this case pertains to male size only. Thus, ultimately, it needs to be shown that pinniped *male* size is correlated with sexual competition. However, a possible effect on female size is interesting for several reasons. For instance, in a phylogenetic study on size dimorphism in primates Lindenfors and Tullberg (1998) were able to show that as the degree of polygyny increased, so did both male and female size. Sexual size dimorphism evolved as a result of this size increase being more pronounced for males. Moreover, for several groups of organisms an allometric relationship is found between male and female size, where, in species with male-biased dimorphism, a higher degree of dimorphism is found in larger species ("Rensch's rule": Rensch 1950, 1959; Abouheif and Fairbairn 1997; Fairbairn 1997). This positive correlation between size and size dimorphism is expected for theoretical reasons, because when selection acts for larger or smaller size in one sex, genetic correlations can lead to a change in size in the other sex as well (Maynard Smith 1978; Lande 1980, 1987; Lande and Arnold 1983). It is thus interesting to see if pinniped size evolution also follows this pattern.

Methods

Sex-specific data for body lengths and body weights were gathered from the literature. Data on average male harem sizes were collected with species classified as monogamous or serially

monogamous denoted as having a harem size of one. See the Appendix for data and data sources. We also carried out similar analyses to those presented here on sex ratios derived from a categorical classification of mating systems (Riedman 1998), but as these gave very similar results they were excluded from the presentation. All data were log-transformed prior to analysis. Dimorphism was thus calculated as log(male size/female size) which equals log(male size) - log(female size) resulting in problems with using ratios in statistical calculations being overcome.

The phylogeny used in the analyses is the pinniped subsection of a composite phylogeny of the Carnivora (Bininda-Emonds et al. 1999) derived with a super-tree technique combining a large number of source phylogenies, both molecular and morphological. Note here that there are too few pinniped species for any meaningful examination of phocids and otariids separately.

We used Felsenstein's (Felsenstein 1985) independent contrasts method as implemented in the computer program PDAP (Garland et al. 1993). Polytomies were handled by using zero-length branches (Felsenstein 1985). All branch lengths were set to unity. Prior to using the contrasts method diagnostics as described by Garland et al. (1992) were carried out. As these diagnostics revealed no significant trends in the data no adjustments of the branch lengths were needed.

When analysing the relationship between male and female body size evolution, major axis regressions were used because there is no hypothesis of causation for pinnipeds stating that one sex is driving size evolution. For the analyses relating harem size to male and female body size as well as body size dimorphism, ordinary regressions were employed for the related reason that here the hypothesis is that harem size is the selective factor acting on the other two.

Results

Major axis regressions through the origin on male and female body size contrasts reveal that size evolution of the two sexes is significantly correlated, both when length (b=1.117, P<0.001, R^2=0.494, n=36) and weight (b=1.242, P<0.001, R^2=0.580, n=37) are used as measures of body size. Neither of these slopes is significant-

Fig. 3 The regression lines through the origin on harem size and **a** length contrasts and **b** weight contrasts. There is clearly no influence of harem size on female size, while there is a significant relationship between harem size and male size
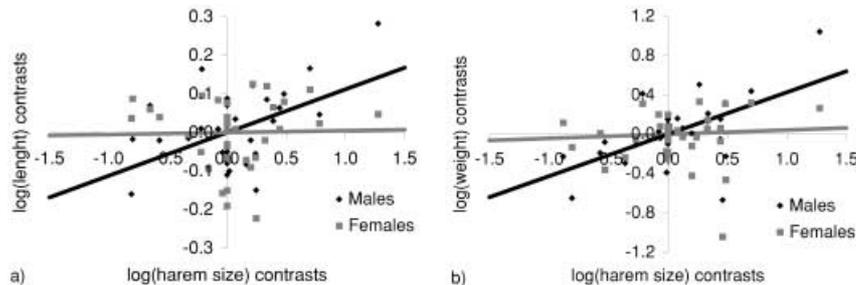
ly different from a slope of 1.0 ($P>0.05$). Thus, no significant relationship between body size and sexual size dimorphism could be found (Fig. 1).

Independent contrasts analyses clearly show that size dimorphism is positively correlated with harem size, both when body size is measured as length ($b=0.106$, $P<0.001$, $R^2=0.385$, $n=35$) and as weight ($b=0.382$, $P<0.001$, $R^2=0.572$, $n=36$) (Fig. 2).

As predicted by sexual selection theory, male body size is positively correlated with harem size, both when body size is measured as length ($b=0.112$, $P=0.002$, $R^2=0.243$, $n=35$) and weight ($b=0.426$, $P<0.001$, $R^2=0.303$, $n=36$). However, we can find no corresponding relationship of female body size and harem size, either when body size is measured as length ($b=0.005$, $P=0.890$, $R^2=0.001$, $n=35$), or when body size is measured as weight ($b=0.042$, $P=0.703$, $R^2=0.004$, $n=36$) (Fig. 3). These results lend substantial support to the hypothesis that sexual size dimorphism in pinnipeds is a result of selection working on males alone.

Discussion

One result from this study is that we found no significant allometric relationship between male and female size. Thus, for pinnipeds there is no significant increase in sexual size dimorphism with body size, which is in contrast to several other groups of animals where this is the case (Abouheif and Fairbairn 1997; Fairbairn 1997; Lindenfors and Tullberg 1998). However, because the slope for pinnipeds has a value that exceeds 1.0, if not significantly so (Fig. 1), one could say that our result nevertheless is in agreement with a general trend supporting Rensch's rule found in the comparative analysis by Abouheif and Fairbairn (1997).

The significant relationship between sexual selection as measured by harem size and sexual size dimorphism is important in that it confirms, using phylogenetically independent contrasts, a pattern that has previously only been shown on a species-by-species basis (e.g. Alexander et al. 1979; Boness et al. 1991; Kovacs and Lavigne 1992; Weckerly 1998). Most importantly, however, we have demonstrated a relationship between the degree of sexual selection on males and male body size per se. As sexual size dimorphism hypothetically can be a result of various selection pressures, on females as well as on males (e.g. Price 1984; Arak 1988; Blackenhorn 2000), this specific

result provides stronger support for the theory of sexual selection than would a correlation between harem size and size dimorphism alone.

All seals do not have the potential to evolve a polygynous mating system. To a large degree the determining factor behind pinniped mating systems is the female grouping pattern (e.g. Bartholomew 1970; Riedman 1998 and references cited therein). Almost all land-breeding species aggregate seasonally on beaches where it is possible for males to defend areas which represent a resource for pregnant females in terms of their suitability as pupping sites. In contrast, almost all species of ice-breeding pinnipeds, both those breeding on floating ice and those breeding on ice attached to land, are monogamous or only slightly polygynous. Ice-breeding female pinnipeds have access to potentially larger breeding areas, especially if they can maintain breathing and access holes through the ice. They are therefore more dispersed than land-breeding females, and in many cases they have a dramatically contracted lactation period (e.g. 4 days in the Hooded seal, *Cystophora cristata*: Bowen et al. 1985). This dispersal is likely to result in difficulties for males to monopolise several females.

Since this strong correlation between breeding habitat and mating system exists (e.g. Bartholomew 1970; Riedman 1998), the breeding habitat is a statistically confounding factor for the present study that cannot be factored out of the analyses, and its effect cannot be analysed separately. The question to ask is therefore if breeding habitat in itself could act as a selective factor on male size and, as a consequence, on size dimorphism. Such a relationship is hard to imagine, however. Pinnipeds spend almost all their lives, and forage, in the water, so a brief ecological advantage during breeding could constitute only a small natural selection pressure.

Interestingly, and in sharp contrast to the pattern in primates (Lindenfors and Tullberg 1998) and many other animals (Abouheif and Fairbairn 1997), we found no relationship between the degree of sexual selection on males and the body size of females. This indicates that male and female sizes are decoupled with respect to the response to sexual selection on males. Note that male and female size evolution is closely correlated *in general* in pinnipeds, but not when the size change is due to sexual selection.

A correlated response in females to selection acting on males should be the result of any existing genetic correlation, but it is expected to be a temporary phenome-

non occurring before females reach their own optimal size (Maynard Smith 1978; Lande 1980, 1987; Lande and Arnold 1983). Alternatively, a correlated response should be the result of any existing correlational selection, for instance if larger females produce larger sons (Fairbairn 1997). For example, it has been shown that the size of female southern elephant seals (*Mirounga leonina*) to a large degree influences the size of their offspring and that males are larger than females at birth. In fact, females smaller than a certain size threshold do not give birth to *any* male pups (Arnbom et al. 1994). Conflicting evidence exist for the northern elephant seals (*Mirounga angustirostris*) as well as for grey seals (*Halichoerus grypus*). For instance, Smiseth and Lorentsen (1995) suggested that maternal expenditure did not differ between male and female pups, although suckling rate, a component shown to be of significant importance in fallow-deer (*Cervus dama*) (Birgersson et al. 1998) and of potential importance in all mammals, was not measured in that study. In contrast, Kovacs and Lavigne (1986) and Anderson and Fedak (1987) both reported that birth mass, growth rate, and mass at weaning were all higher for male than for female pups, although maternal mass was not controlled for in either of these studies.

In otariids the pattern is also far from clear. Studies generally seem to indicate that male pups are heavier at birth and grow slightly faster, but that they do not receive more milk than female pups. For instance, Arnould et al. (1996) showed that although male and female Antarctic fur seal (*Arctocephalus gazella*) pups received equal amounts of milk, males directed more of this to lean tissue growth while females accumulated greater adipose stores. Since fat and lean tissue differ in terms of density and energy content, a lighter but fatter pup may still have received the same amount of energy and material from its mother as a bigger, heavier pup. In California sea lions (*Zalophus californianus*), however, dimorphism is reported to result from differential maternal expenditure in the two sexes (Ono and Boness 1996).

In general, the evidence for differential expenditure in the sexes seems rather tenuous (Trillmich 1996). Even for species in which the evidence for differential expenditure is convincing, the fitness returns in terms of future survival and reproduction have not been measured.

We can only conclude that factors related to sexual selection on males are of little importance in determining pinniped female size. Explanations for female size changes thus have to be investigated in another context. Selection for female size is likely driven by a complex set of trade-offs between factors such as lactation patterns, prey availability and a balance between immediate costs of lactation (in terms of energy depletion) and future reproductive performance of females as well as offspring (e.g. Costa 1991; Boyd 1998; Pomeroy and Fedak 1999). This discussion is, however, outside the scope of the present paper.

Appendix

Overview of data collected

Species	Harem size	Male weight (kg)	Female weight (kg)	Male length (cm)	Female length (cm)	Harem size reference	Body size reference
Monachus schauinslandi	1	173.00	265.00	214.20	233.70	Riedman 1998	Bininda-Emonds and Gittleman 2000
Monachus monachus	1	260.00	301.00	254.75	364.60	Riedman 1998	Bininda-Emonds and Gittleman 2000
Mirounga angustirostris	13	2275.00	513.00	450.00	295.00	Alexander et al. 1979	Bininda-Emonds and Gittleman 2000; Female weight: Costa 1993
Mirounga leonina	48	3510.00	503.00	467.00	270.00	Alexander et al. 1979	Bininda-Emonds and Gittleman 2000
Leptonychotes weddelli	3	360.00	376.00	250.00	259.50	Alexander et al. 1979	Bininda-Emonds and Gittleman 2000
Ommatophoca rossi	1	173.80	185.00	199.00	214.60	Laws and Hofman 1979	Bininda-Emonds and Gittleman 2000
Lobodon carcinophagus	1	220.50	224.00	226.00	228.50	Riedman 1998	Bininda-Emonds and Gittleman 2000
Hydrurga leptonyx	1	324.00	367.00	287.00	322.48	Alexander et al. 1979	Bininda-Emonds and Gittleman 2000
Cystophora cristata	1	343.18	222.50	260.00	206.00	Riedman 1998	Bininda-Emonds and Gittleman 2000
Erignathus barbatus	1	265.00	276.36	230.00	230.00	Riedman 1998	Bininda-Emonds and Gittleman 2000
Halichoerus grypus	5	233.00	155.00	216.35	180.00	Boness et al. 1995	Bininda-Emonds and Gittleman 2000
Phoca groenlandica	1	135.00	129.50	176.00	169.30	Lavigne 1979	Bininda-Emonds and Gittleman 2000

Appendix (continued)

Species	Harem size	Male weight (kg)	Female weight (kg)	Male length (cm)	Female length (cm)	Harem size reference	Body size reference
Phoca fasciata	1	94.80	80.36	153.00	154.70	Stirling 1979	Bininda-Emonds and Gittleman 2000
Phoca largha	1	97.00	86.00	168.95	159.00	Riedman 1998	Bininda-Emonds and Gittleman 2000
Phoca caspica	1	70.50	55.00	150.00	136.40	Riedman 1998	Bininda-Emonds and Gittleman 2000
Phoca sibirica	1	89.50	89.50	130.00	125.35	Riedman 1998	Bininda-Emonds and Gittleman 2000
Phoca hispida	1	71.67	66.50	129.30	128.90	Riedman 1998	Bininda-Emonds and Gittleman 2000
Phoca vitulina vitulina	1	80.00	66.00	145.00	137.50	Bonner 1979	Bonner 1982
Phoca vitulina richardsi	1	87.60	64.80	161.60	147.70	Bonner 1979	Bonner 1979
Phoca vitulina stejnegeri	1	128.50	101.00	180.00	164.50	Bonner 1979	Bigg 1981
Zalophus californianus californianus	16.2	289.00	86.00	225.00	180.00	Kovacs and Lavigne 1992	Weight: Kovacs and Lavigne 1992; length: Bininda-Emonds and Gittleman 2000
Zalophus californianus wollebaeki	13.5	200.00	78.00			Kovacs and Lavigne 1992	Kovacs and Lavigne 1992
Eumetopias jubatus	11.8	1000.00	287.55	300.00	240.15	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Otaria byronia/flavescens	6	300.00	144.00	234.88	188.86	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Neophoca cinerea	3.8	300.00	78.55	212.50	148.20	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Phocartos hookeri	12.9	364.00	183.00	225.00	180.00	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Callorhinus ursinus	36.4	227.00	44.75	213.00	135.00	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Arctocephalus townsendi	6.2	145.00	49.55	200.30	141.60	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Arctocephalus philippii		140.00	50.00	200.00	140.00		Bininda-Emonds and Gittleman 2000
Arctocephalus galapagoensis	5.9	64.50	27.40	151.25	120.00	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Arctocephalus australis	6	159.00	48.50	189.25	141.25	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Arctocephalus forsteri	6.2	164.38	55.00	199.38	141.88	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Arctocephalus gazella	10.3	155.00	38.20	185.90	128.75	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Arctocephalus tropicalis	6.5	152.50	50.00	180.00	145.00	Kovacs and Lavigne 1992	Bininda-Emonds and Gittleman 2000
Arctocephalus pusillus pusillus	28.9	278.00	71.00	253.50	181.50	Kovacs and Lavigne 1992	Kovacs and Lavigne 1992
Arctocephalus pusillus doriferus	10.5	307.00	84.00	215.60	157.20	Kovacs and Lavigne 1992	Kovacs and Lavigne 1992
Odobenus rosmarus rosmarus	5	1050.00	655.00	300.00	250.00	Kovacs and Lavigne 1992	Kovacs and Lavigne 1992
Odobenus rosmarus divergens	9.4	1353.00	738.00	315.20	260.60	Kovacs and Lavigne 1992	Kovacs and Lavigne 1992

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