Sexual selection uncouples the evolution of brain and body size in pinnipeds

J. L. FITZPATRICK*, M. ALMBRO*, A. GONZALEZ-VOYER†, S. HAMADA*, C. PENNINGTON*, J. SCANLAN* & N. KOLM‡

*Centre for Evolutionary Biology, School of Animal Biology, University of Western Australia, WA, Australia
†Department of Integrative Ecology, Estación Biológica de Doñana – Consejo Superior de Investigación Científica (CSIC), Sevilla, Spain
‡Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

Abstract

The size of the vertebrate brain is shaped by a variety of selective forces. Although larger brains (correcting for body size) are thought to confer fitness advantages, energetic limitations of this costly organ may lead to trade-offs, for example as recently suggested between sexual traits and neural tissue. Here, we examine the patterns of selection on male and female brain size in pinnipeds, a group where the strength of sexual selection differs markedly among species and between the sexes. Relative brain size was negatively associated with the intensity of sexual selection in males but not females. However, analyses of the rates of body and brain size evolution showed that this apparent trade-off between sexual selection and brain mass is driven by selection for increasing body mass rather than by an actual reduction in male brain size. Our results suggest that sexual selection has important effects on the allometric relationships of neural development.

Introduction

Evolutionary biologists since Darwin (1871) have sought to explain the conspicuous variation in relative (i.e. body-size-corrected) brain size observed across species. Yet understanding the selective factors that influence investment in neural tissue is challenging as the complexity and significance of the brain in biological systems means that brain evolution is shaped by multiple selective forces simultaneously (Healy & Rowe, 2007; Dechmann & Safi, 2009). Indeed, there is now compelling evidence that a wide range of ecological, life-history, physiological, social and sexually selected pressures influence relative brain size across a wide range of taxa (Dunbar, 1998; Kotrschal *et al.*, 1998; Hutcheon *et al.*, 2002; Reader & Laland, 2002; Lefebvre *et al.*, 2004; Pitnick *et al.*, 2006; Gonzalez-Voyer *et al.*, 2009; Gonzalez-Voyer & Kolm, 2010). However, a critical, but understudied, evolutionary consideration in brain evolution is that the magnitude and direction of evolutionary responses in brain size can be sex-specific, as the

Correspondence: John Fitzpatrick, Centre for Evolutionary Biology, School of Animal Biology (M092), University of Western Australia, Crawley, 6009 WA, Australia.
Tel.: +61 8 6488 1773; fax: +61 8 6488 1029;
e-mail: jfitzpat@cyllene.uwa.edu.au

cognitive demands and constraints associated with physiological, ecological, social and sexual factors can differ dramatically between the sexes (Jacobs, 1996). Yet, as few studies have investigated how intersexual differences in naturally and sexually selected pressures influence investment in neural tissue (e.g. Garamszegi *et al.*, 2005; Lindenfors *et al.*, 2007; Gonzalez-Voyer *et al.*, 2009; Gonzalez-Voyer & Kolm, 2010), we consequently know very little about sex-specific evolutionary responses in relative brain size. Therefore, making sense of how selection acts on brain evolution necessitates an integrated, sex-specific approach that simultaneously evaluates multiple factors that are hypothesized to influence brain evolution (Healy & Rowe, 2007; Dechmann & Safi, 2009).

Typically, investment in neural tissue above what would be predicted for a given body size is assumed to confer an evolutionary advantage (Byrne & Whiten, 1997; Dunbar, 1998; Dunbar & Shultz, 2007), as relatively large-brained individuals are assumed to have enhanced cognitive capabilities (Allman *et al.*, 1993; Allman, 2000). However, investment in relatively larger brains is costly, as the development and maintenance of neural tissue is metabolically expensive (Aiello & Wheeler, 1995). Therefore, evolutionary trade-offs are expected between investment in neural tissue and other

metabolically costly tissues (termed the 'expensive tissue hypothesis'; Aiello & Wheeler, 1995; Kaufman, 2003; but see Jones & MacLarnon, 2004; Isler & van Schaik, 2006a). Building on this idea, Pitnick *et al.* (2006) developed the 'expensive sexual tissue hypothesis', which suggests that investment in expensive sexually selected traits (e.g. testicular tissue) can limit investment in neural tissue. However, recent assessments of how sexual selection influences brain evolution in vertebrates have produced contradictory results (Garamszegi *et al.,* 2005; Pitnick *et al.*, 2006; Lindenfors *et al.*, 2007; Guay & Iwaniuk, 2008; Lemaître *et al.*, 2009; Gonzalez-Voyer & Kolm, 2010), and consequently, the importance of sexual selection in shaping brain evolution remains controversial (Dechmann & Safi, 2009; Lemaître *et al.*, 2009).

Here, we examine the patterns of selection on relative (i.e. correcting for body mass) male and female brain size in pinniped (seals, sea lions and walruses). Pinnipeds are an excellent model for studying brain evolution, as the wealth of ecological, physiological and life-history data readily available (e.g. Kovacs & Lavigne, 1986, 1992; Bininda-Emonds & Gittleman, 2000; Lindenfors *et al.*, 2002; Schulz & Bowen, 2004; Ferguson, 2006) facilitates an integrated assessment of the selective forces that may influence brain evolution. We assessed whether relative investment in male and female brain size in pinnipeds is influenced by multiple selective forces hypothesized to influence the brain evolution, including social factors, maternal energy constraints, lifespan, basal metabolic rate, physiological constraints associated with diving, and trade-offs among expensive tissues (Robin, 1973; Allman *et al.*, 1993; Aiello & Wheeler, 1995; Martin, 1996; Dunbar, 1998; Jones & MacLarnon, 2004; Isler & van Schaik, 2006b; Pitnick *et al.*, 2006; González-Lagos *et al.*, 2010). As pinnipeds exhibit extreme variance in the degree of sexual selection experienced between the sexes – sexual selection is more intense in males than in females – and among species (Bartholomew, 1970; Lindenfors *et al.*, 2002), we also examined whether differences in the intensity of sexual selection generate contrasting patterns of brain evolution among pinnipeds. Most vertebrate taxa exhibit a strong positive relationship between brain and body mass (Jerison, 1973, 1991; Lande, 1979; Striedter, 2005), which is presumed to stem from the fact that larger bodies require larger brains to maintain basic functions (e.g. Aboitiz, 1996). Yet despite this wide-spanning relationship between brain and body mass, under conditions of strong directed selection on either brain or body size, the normally tight association between these traits can become uncoupled (Gonzalez-Voyer & Kolm, 2009). Thus, we investigated whether intense selective pressure to increase male body size in species where males control harems (Alexander *et al.*, 1979; Lindenfors *et al.*, 2002), which represents a substantial energetic demand (Blanckenhorn, 2000), affects the relationship between brain and body size in male, but not female, pinnipeds. After characterizing the

association between relative brain size and various selective factors hypothesized to influence brain evolution separately, we evaluated how sexual selection influences brain evolution in male and female pinnipeds while accounting for potential interactions among these selective factors using multivariate statistical models. Finally, we used recently developed phylogenetic rates of phenotypic diversification tests to disentangle how sexual selection influences the rate of phenotypic diversification in body and brain mass in pinnipeds.

Methods

Data collection

Physiology, life-history, social and ecological data were collected from published literature for all extant pinniped species (n = 33 species, see Supporting information). All data collected are known to be associated with brain evolution in other taxa (see Introduction). Sex-specific data on brain and body mass were compiled, and mean values were used where multiple sources of data were available. Maternal energy constraints and life-history effects on brain evolution were evaluated using data on the duration of lactation, the length of gestation and species mean values for adult lifespan. Physiological constraints on brain evolution were evaluated using data on basal metabolic rate and maximum dive duration. To evaluate the trade-offs among brain mass and other energetically expensive tissues, data were compiled on intestine length (to evaluate the 'expensive tissue hypothesis', Aiello & Wheeler, 1995) and male testes mass (to evaluate the 'expensive sexual tissue hypothesis', Pitnick *et al.*, 2006). Sex-specific data on intestine length values were unavailable, and mean species values are therefore examined. Harem size and sexual size dimorphism (SSD), which are correlated with one another in pinnipeds (Alexander *et al.*, 1979; Lindenfors *et al.*, 2002), were used to estimate the magnitude of sexual selection in this study. Sexual dimorphisms are a commonly used proxy for the strength of sexual selection as several comparative studies across a broad taxonomic range have revealed that high levels of dimorphism are associated with highly polygamous mating systems (e.g. Clutton-Brock *et al.*, 1977; Alexander *et al.*, 1979; Webster, 1992; Dunn *et al.*, 2001; Gonzalez-Voyer *et al.*, 2008). SSD in body mass was calculated from male and female mass data using the formula log(male body mass/female body) (Fairbairn, 2007). Population density was used as a proxy measure for social encounters (to evaluate the 'social brain' hypothesis, Dunbar, 1998). We only considered population density values taken from outside the breeding areas (Bininda-Emonds & Gittleman, 2000) as breeding aggregations can be incredibly dense and harem size provides a measure of the number of adult individuals likely encountered in breeding areas.

Phylogenetic linear models

The relationship between brain mass and various predictor variables was assessed in a series of phylogenetically controlled linear models. To account for the evolutionary relationships among species, phylogenetically controlled generalized least-squared (PGLS) regression analyses (Freckleton *et al.*, 2002) were performed using log-transformed data in the APE package of the statistical program R v. 2.13.1 (R Development Core Team, 2011). Log-transformed data were used to equalize variances and linearize data. PGLS regressions estimate a maximum-likelihood value of the phylogenetic scaling parameter λ. The λ parameter estimates the effect of shared ancestry on the relationship between brain size and the factors analysed (Pagel, 1999; Freckleton *et al.*, 2002). Thus, PGLS regressions evaluate the phylogenetic relationships on the covariance in the residuals in the model ($\lambda = 0$ denotes no phylogenetic signal, and $\lambda = 1$ denotes strong phylogenetic signal). For all analyses, the phylogenetic relationship among pinniped species was accounted for using a molecular supertree, including branch lengths, kindly provided by Jeff Higdon (Higdon *et al.*, 2007).

The relationship between male and female brain mass and physiological, life-history and ecological variables was initially assessed using separate multiple regressions with body mass added as a covariate in all analyses to account for allometric effects (García-Berthou, 2001; Freckleton, 2002). However, the use of separate regression models raises several important statistical issues. Specifically, performing multiple tests using the same variables can increase the incidence of type I errors, does not account for association among predictor variables and may either fail to detect relationships, as the effects only become apparent when accounting for other predictor variables, or may reveal an apparent pattern of selection that is in fact attributed to another, unexamined, variable. Nevertheless, we began our analysis with separate regression models because our aim was to assess as many factors hypothesized to influence the brain evolution in pinnipeds as possible and the sample sizes for the various predictor variables differed greatly, thus precluding a multiple regression that evaluated all hypotheses simultaneously. Therefore, despite their limitations, we included these separate regressions in order to evaluate the relative effect of as many predictor variables on brain size evolution in pinnipeds as possible. While we refrain from overinterpreting these results due to the statistical limitations outlined above, we hope that their inclusion will shed light on and stimulate further investigation of the selective factors that influence the brain size evolution in pinnipeds.

Because brains are subject to a wide range of selective pressures that act simultaneously (Healy & Rowe, 2007; Dechmann & Safi, 2009), we next assessed how multiple predictor variables influence brain size in a multivariate

context. The availability of data on physiological, life-history and ecological variables differed among pinnipeds species. Therefore, sex-specific multivariate statistical tests were performed on a subset of $n = 23$ pinniped species, representing 70% of extant pinnipeds, where data on brain and body mass and seven predictor variables hypothesized to influence the brain evolution were available for males and females. The predictor variables examined in the multivariate tests included harem size, gestation length, lifespan, lactation duration, maximum dive duration, SSD and the age of sexual maturity for males (in male analyses) and females (in the female analyses). We then performed sex-specific phylogenetic multiple regressions on these seven predictor variables while including body mass as a covariate in the models.

However, multiple regression models may not accurately assess individual predictor variables in cases where there is colinearity or multicolinearity between predictor variables, as is the case among some predictor variables in pinnipeds (e.g. SSD and harem size, Lindenfors *et al.*, 2002). Therefore, we also used phylogenetic principal component analyses (PPCA, Revell, 2009) to combine the seven physiological, life-history and ecological variables into a reduced set of orthogonal components. PPCA transform data into principal components while incorporating phylogenetic effects (Revell, 2009). This approach reduces type I error rates when performing subsequent phylogenetically controlled analyses on principal components and accounts for statistical issues arising from multicolinearity among predictor variables (Revell, 2009). Male and female PPCA each returned three principal components with eigenvalues > 1, which were considered in further analyses (Table 1). For both sexes, sexually selected traits (harem size and SSD) loaded strongly and positively on the first principal component (PC1), whereas life-history traits (lactation duration and age of maturity) primarily loaded on the second principal component (PC2) and lifespan loaded heavily on the third principal component (PC3) (Table 1). We then applied multiple regression analyses to male and female brain size using the three sex-specific orthogonal principal components with eigenvalues > 1 as independent variables and body size as a covariate.

Finally, we performed sex-specific phylogenetic ANCOVAs to contrast the relationship between brain and body mass in species with and without harems. Species where males did not control harems were classified as experiencing 'low' levels of sexual selection, whereas species where males control harems were classified as experiencing 'high' levels of sexual selection.

Comparing rates of body and brain mass evolution

To assess how sexual selection influences the rate of phenotypic evolution in body and brain mass, we categorized species into 'low' (species without harems)

Table 1 Principal component analysis of ecological, life-history and sexually selected variables for (a) male and (b) female pinnipeds.

| Trait | Phylogenetic principal components | | |
	PC1	PC2	PC3
(a) Males			
Harem size	**0.53**	−0.27	0.27
Sexual size dimorphism	**0.60**	−0.04	−0.14
Lactation duration	−0.19	**−0.67**	−0.13
Male age of maturity	−0.0004	**−0.57**	−0.18
Lifespan	−0.21	0.06	**0.78**
Maximum dive duration	0.40	−0.18	0.42
Gestation length	−0.34	−0.35	0.27
Eigenvalue	2.09	1.43	1.16
(b) Females			
Harem size	**0.50**	−0.42	0.05
Sexual size dimorphism	**0.60**	−0.09	0.21
Lactation duration	−0.21	**−0.46**	0.59
Female age of maturity	−0.14	**−0.57**	−0.18
Lifespan	−0.25	−0.35	**−0.64**
Maximum dive duration	0.38	−0.28	−0.28
Gestation length	−0.35	−0.30	0.30
Eigenvalue	2.12	1.50	1.19

Eigenvectors shown in boldface are > 70% of the largest eigenvector and contributed significantly to the PC (Mardia *et al.*, 1979).

or 'high' (species with harems) sexual selection groups (as above). The ancestral states of sexual selection were reconstructed using the maximum-likelihood Mk1 model in MESQUITE version 2.75 (Maddison & Maddison, 2011). Branches in the phylogeny were assigned to either low or high sexual selection based on ancestral state reconstruction analyses (see Supporting information). We then used phenotypic diversification rate tests to compare the rates of diversification in body and brain mass for male and female pinnipeds between the two sexual selection groups. All analyses were performed using the MOTMOT package (Thomas & Freckleton, 2012) in R v. 2.13.1 (R Development Core Team, 2011). To compare the rate of phenotypic diversification between the sexual selection groups, we applied a scalar, θ, to the high sexual selection group. The maximum-likelihood estimate of θ was estimated, where deviations from $\theta = 1$ are indicative of differences in the rate of trait evolution between the sexual selection groups (Thomas *et al.*, 2009). For all analyses, θ was rescaled such that the low sexual selection group was $\theta = 1$. Thus, for the high sexual selection group, θ values greater than one indicate comparatively rapid rates of trait diversification (compared to the low sexual selection group), whereas θ values less than one indicate comparatively slow rates of trait diversification. The 95% confidence intervals 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 we also performed our analyses assuming a common phylogenetic mean, we found qualitatively similar results (data not shown).

Results

Separate multiple regressions controlling for body mass revealed sex-specific responses in relative (i.e. body-size-corrected) brain mass to the predictor variables examined. In males, relative brain mass was negatively correlated with maximum dive duration (Table 2), and there was a statistical trend suggesting that relative male brain mass is smaller in species with more intense male-biased SSD (Table 2). In females, relative brain mass was positively correlated with population density (Table 2). For both sexes, the remainder of the multiple regressions did not reveal significant associations between relative brain mass and any of the other predictor variables examined (Table 2). However, we were concerned with possible spurious correlations that may have arisen given the large number of separate tests performed when evaluating the relationship between brain size and the predictor variables in Table 2. Therefore, although biologically interesting, we refrain from overinterpreting the results of these separate phylogenetic regressions.

Multivariate tests that examined the relationship between relative brain size and seven predictor variables (harem size, gestation length, lifespan, lactation duration, maximum dive duration, SSD and the age of sexual maturity, while controlling for the allometric effects of body mass) also revealed sex-specific responses in

Table 2 Regression models of brain mass in relation to various predictor variables for males and females when controlling for phylogeny (PGLS). Body mass was added as a covariate and was significantly positively related to brain mass in all models. The sample size, partial regression slopes (β) for the predictor variable and *P*-values are presented for each model. Full statistical details of the models are available in the Supporting information.

| Predictor variable | Males | | | Females | | |
	n	β	*P*	*n*	β	*P*
Harem size	31	−0.05	0.40	30	0.04	0.32
Sexual size dimorphism	31	−0.17	0.09	30	0.13	0.13
Testes mass	13	0.09	0.32	–	–	–
Lactation duration	30	0.03	0.58	30	0.03	0.56
Age of sexual maturity	30	< 0.01	0.74	29	< 0.01	0.78
Lifespan	29	−0.05	0.78	29	−0.15	0.28
Population density	13	0.02	0.65	14	0.08	**0.04**
Maximum dive duration	26	−0.15	**0.01**	25	−0.07	0.33
Gestation length	29	0.06	0.87	29	−0.38	0.23
Basal metabolic rate	8	0.28	0.21	8	0.35	0.13
Small intestine length	17	0.03	0.74	17	−0.03	0.63
Large intestine length	11	0.20	0.17	11	0.06	0.49

Table 3 Phylogenetically controlled PGLS multiple regression models of the relationships between brain mass and multiple physiological, life-history and ecological variables for (a) male and (b) female pinnipeds.

Trait	λ	d.f.	Predictor	β	t	P
(a) Males						
Brain mass	$< 0.001^{ns,*}$	14	Body mass	0.52	6.10	**< 0.001**
			Harem size	0.09	1.04	0.32
			Sexual size dimorphism	−0.31	−1.87	0.08
			Lactation duration	−0.04	−0.59	0.56
			Female age of maturity	0.00	0.64	0.54
			Lifespan	−0.19	−1.08	0.30
			Maximum dive duration	−0.21	−2.45	**0.03**
			Gestation length	0.11	0.13	0.90
(b) Females						
Brain mass	$< 0.001^{ns,ns}$	14	Body mass	0.47	5.12	**< 0.001**
			Harem size	0.10	1.05	0.31
			Sexual size dimorphism	0.02	0.11	0.92
			Lactation duration	−0.03	−0.41	0.69
			Female age of maturity	0.00	0.28	0.78
			Lifespan	−0.38	−1.71	0.11
			Maximum dive duration	−0.15	−1.76	0.10
			Gestation length	0.77	0.87	0.40

PGLS, phylogenetically controlled generalized least-squared.
Superscripts after the phylogenetic scaling parameter, λ, indicate whether 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 '*'. Partial regression slopes (β) are presented for each predictor variable. Significant relationships are presented in bold text.

relative brain mass. Phylogenetically controlled multiple regression for male pinnipeds demonstrated that the relative mass of male brains was negatively correlated with maximum dive duration and offered suggestive evidence of a negative correlation between relative brain mass and the degree of male SSD (Table 3a). In contrast, female relative brain mass was not correlated with any of the seven predictor variables examined in the phylogenetically controlled multiple regression (Table 3b). Incidentally, for both sexes, these results closely match those obtained in the separate regression analyses reported in Table 2.

Sex-specific phylogenetically controlled multiple regressions that assessed three principal components generated from a PPCA and body mass were then used to account for correlations among the predictor variables. These tests revealed that relative male brain mass was negatively associated with PC1 (Table 4a), the principal component that was primarily loaded by sexually selected traits (see Table 1). Therefore, for males, the PPCA strengthened the patterns of selection uncovered in the multiple regression presented in Table 3. For females, there were no statistically significant associations between any of the principal components and

Table 4 Phylogenetically controlled PGLS multiple regression models of the relationships between brain mass and multiple physiological, life-history and ecological variables summarized using phylogenetic principal component analyses for (a) male and (b) female pinnipeds.

Trait	λ	d.f.	Predictor	β	t	P
(a) Males						
Brain mass	$< 0.001^{ns,*}$	18	Body mass	0.50	8.48	**< 0.001**
			PC1-sexually selected traits	−0.008	−2.22	**< 0.001**
			PC2-life-history traits	−0.001	−0.43	0.67
			PC3-lifespan	−0.007	−1.69	0.11
(b) Females						
Brain mass	$0.75^{ns,*}$	18	Body mass	0.39	6.25	**< 0.001**
			PC1-sexually selected traits	0.002	0.59	0.56
			PC2-life-history traits	−0.001	−0.33	0.75
			PC3-lifespan	0.006	1.57	0.13

PGLS, phylogenetically controlled generalized least-squared.
Superscripts after the phylogenetic scaling parameter, λ, indicate whether 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 '*'. Partial regression slopes (β) are presented for each predictor variable. Significant relationships are presented in bold text.

female brain mass after accounting for allometric effects (Table 4b).

Phylogenetic ANCOVAs revealed that the relationship between brain and body mass differed between sexual selection groups (i.e. species with or without harems) in males but not females. In male pinnipeds, a significant interaction term revealed that differences in male brain size between the sexual selection groups were dependent on male body size ($\lambda < 0.001$, male mass: $t_{27} = 8.51$, $P < 0.001$; sexual selection group: $t_{27} = -3.23$, $P = 0.003$; male mass*sexual selection group: $t_{27} = 3.24$, $P = 0.003$, Fig. 1a). Specifically, compared to species where males did not hold harems, in harem holding species males have relatively large brains when male body mass is low and males have relatively smaller brains when body mass is high. In female pinnipeds, the relationship between brain and body mass did not differ between the sexual selection groups ($\lambda = 0.88$, female mass: $t_{26} = 5.92$,
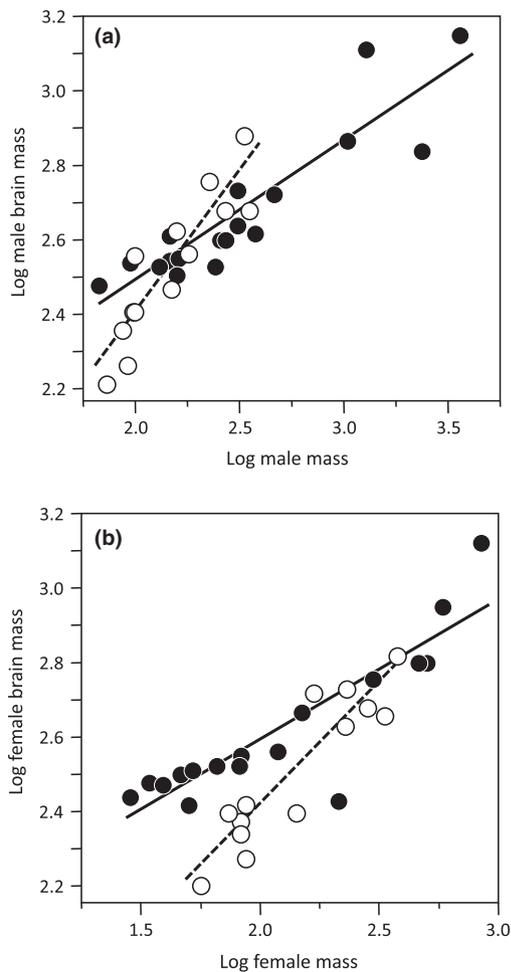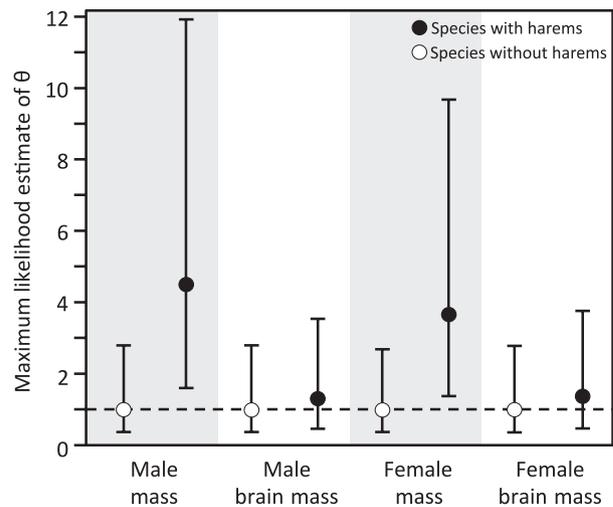
Fig. 2 Rates of diversification of body and brain mass for male and female pinnipeds. The maximum-likelihood estimates of the relative rate of diversification (θ) and their 95% confidence intervals are shown for four traits: male body mass, male brain mass, female body mass and female brain mass. Each trait is divided into species without harems (open circle) or species with harems (filled circle). The dashed line shows $\theta = 1$ values: for all models, the θ value was rescaled so that the low sexual selection group had $\theta = 1$.

$P < 0.001$; sexual selection group: $t_{26} = -0.69$, $P = 0.50$; female mass*sexual selection group: $t_{26} = 0.65$, $P = 0.52$, Fig. 1b).

In the analysis of rates of phenotypic evolution, the maximum-likelihood estimate of θ was significantly greater for male ($\chi_1^2 = 7.72$, $P = 0.005$) and female ($\chi_1^2 = 6.47$, $P = 0.01$) body mass in the high sexual selection group than in the low sexual selection group (Fig. 2). In contrast, absolute brain mass did not differ between the low and high sexual selection groups for either sex (males: $\chi_1^2 = 0.28$, $P = 0.59$; females: $\chi_1^2 = 0.40$, $P = 0.53$; Fig. 2). These results indicate that the rate of phenotypic evolution in male and female body size is greater in high sexual selection groups, whereas the rate of phenotypic evolution in brain size was not influenced by sexual selection. Hence, pinniped brain and body mass showed highly distinct rates of phenotypic evolution under the influence of sexual selection.

Discussion

Our multivariate analyses of predictor variables hypothesized to influence brain evolution demonstrated sex-specific responses in relative brain mass in pinnipeds. In male pinnipeds, multiple regressions using phylogenetically controlled principal components revealed a negative relationship between residual brain mass and SSD. Incidentally, such a relationship was also suggested in male pinnipeds from multiple regression analyses, but was not statistically significant. Thus, the use of PPCA in this study highlights the importance of simultaneously

Fig. 1 The relationship between brain and body mass in (a) male and (b) female pinnipeds. Pinnipeds are divided into those species with harems (filled circles, solid line) and those without harems (open circles, broken line).

evaluating multiple predictor variables hypothesized to influence brain evolution, while also accounting for covariance between these predictor variables, in order to uncover how selection acts on brain size. However, interpreting the negative relationship between relative male brain size and the strength of sexual selection requires a better understanding of how selection operates on brains and body mass in pinnipeds. Male pinnipeds may have relatively smaller brains in species where sexual selection in intense due to investment in extreme body mass resulting in a decoupling of the generally strong covariance in evolutionary responses in brain and body mass (sensu Gonzalez-Voyer & Kolm, 2009). Such uncoupling of the normally tight association between brain and body size can occur when selection for either brain or body size is particularly intense. For example, Gonzalez-Voyer & Kolm (2009) recently demonstrated that brain and body size presented highly distinct rates of evolution during the adaptive radiation of Tanganyikan cichlid fishes. Our analysis of the rates of phenotypic evolution in brain and body size in pinnipeds suggests that a similar uncoupling of brain and body size evolution occurs in pinnipeds in response to sexual selection as the rate of diversification of male body mass was greater in species experiencing high levels of sexual selection, whereas the rates of diversification in brain mass did not differ between low and high sexual selection groups. Therefore, the negative relationship between sexual selection and relative brain size in male pinnipeds appears to be driven by an uncoupling of the relationship between brain and body size in pinnipeds.

To our knowledge, this is the first identification of a specific selective force (here sexual selection) strong enough to offset the relationship between brain and body mass. But given the general expectation that more somatic tissues also require more neural tissues, what are the fitness consequences of the apparent decoupling between brain and body mass? In pinniped species with harems, males gain extensive fitness benefits by increasing body size, as larger males have an advantage in male–male competition and are able to become socially dominant (McCann, 1981; Modig, 1996), have longer tenures on harems (Lindstedt & Boyce, 1985) and generally have enhanced mating success (Deutsch et al., 1990; Tinker et al., 1995; Arnould & Duck, 1997). However, increases in male brain size in species with harems may not yield similar fitness benefits. Despite the many potential benefits associated with increasing relative investment in neural tissue (Sol et al., 2005, 2007, 2008; González-Lagos et al., 2010; Amiel et al., 2011; Maklakov et al., 2011), if the brains of male pinnipeds are capable of meeting the cognitive demands associated with their environment, then concomitant increases in brain size with body size may be cognitively unnecessary and may limit the allocation of energy to other traits and activities that have a more direct bearing on fitness. If this were the case, then the negative relationship

between sexual selection and brain size in male pinnipeds could support a more liberal interpretation of Pitnick et al.'s (2006) expensive sexual tissue hypothesis that included extreme investment in body size as a sexual tissue.

In male pinnipeds, simultaneous assessment of seven predictor variables in multiple regression analyses revealed a negative correlation between relative male brain mass and maximum dive duration that appears to support the predictions from the 'dive constraint hypothesis' (Robin, 1973). However, previous studies have questioned the applicability of the dive constraint hypothesis as the notion that having a smaller, less metabolically expensive brain facilitates longer dive durations does not take into account the other physiological adaptations (e.g. increased blood volume and myoglobin levels in muscle tissue) commonly observed in diving marine mammals (Worthy & Hickie, 1986). Moreover, Marino et al. (2006) found that dive constraints do not influence relative brain size investment in cetaceans (whales, dolphins and porpoises) and argued that large muscle mass associated with increased body mass primarily influences the duration of cetacean dives. Indeed, in the present study, the negative relationship between relative brain size and maximum dive duration in males appears to be driven by changes in body size, as is the case in cetaceans (Marino et al., 2006), rather than brain size: absolute male brain size was not correlated with maximum dive duration ($t_{24} = 1.38$, $P = 0.18$), whereas species with larger male body masses dive for longer durations ($t_{26} = 2.36$, $P = 0.03$). Additionally, we could not rule out that the negative relationship between relative male brain size and maximum dive duration was driven by colinearity between dive duration and another predictor variable. To directly address this issue of (multi)colinearity, we used PPCA that instead suggested relative male brain size was negatively related to sexual selection rather than dive constraints.

In contrast to the pattern observed in males, in female pinnipeds, neither sexual selection nor any other predictor variable examined in a multivariate context was related to relative investment in female brain mass. However, as is the case with male pinnipeds, female body mass, but not brain mass, evolved at a rapid rate in pinniped species where males controlled harems and the strength of sexual selection was high. We propose that this effect in females could be caused through the genetic correlation of body size among the sexes. But in females, this apparent uncoupling in the rate of trait evolution does not appear to be sufficient to generate a negative relationship between sexual selection and brain size.

We lacked sufficient data to examine several of the predictor variable hypothesized to influence the brain evolution in a multivariate context. Thus, the examination of these predictor variables (presented in Table 2) should be assessed with caution (see the Methods section for an overview of the statistical limitations of these tests),

and we highlight some results that may be of interest in future investigations of brain evolution in pinnipeds. First, we found no clear support for the predictions of the expensive tissue hypothesis (Aiello & Wheeler, 1995) in either sex or the expensive sexual tissue hypothesis (Pitnick *et al.*, 2006) in male pinnipeds, as investments in digestive and reproductive tissue were not negatively related to relative brain size in this study. Thus, at the level of individual organs, there does not appear to be direct trade-offs with investment in neural tissue and other expensive tissues. A possible alternative explanation may be that brain mass trades-off against energetically expensive adipose tissue, as recently suggested by Navarrete *et al.* (2011). However, as Navarrete *et al.*'s (2011) study did not assess energetic trade-offs between brain size and various organ masses in a multivariate context, the conclusions from their study suffer from the statistical limitations we outlined above. Second, our data suggested that relative female brain size is positively correlated with population density, suggesting that social factors may be an important selective force influencing brain size in female pinnipeds (Dunbar, 1998; Lindenfors *et al.*, 2007). Further investigation of these predictor variables would be of interest. However, at present, it remains unclear how energetic tissues and social factors influence brain size evolution in pinnipeds as there were insufficient data to include this variable in the multivariate analyses.

In conclusion, our results demonstrate a negative relationship between relative brain size in males and the level of sexual selection and suggest that sexual selection has lead to a decoupling in the rate of evolution in brain and body mass in male, but not female, pinnipeds. Sexual selection may therefore impose limits on the cognitive capabilities of males through trade-offs between energetically expensive neural tissue and extreme investment in body size. To assess this hypothesis, a better understanding of how brain size impacts fitness in pinnipeds is required. Just as the strength of sexual selection differs between the sexes (Lindenfors *et al.*, 2002), the evolutionary pressures and trade-offs that influence brain size also appear to be sex-specific in pinnipeds.

Acknowledgments

References

Aboitiz, F. 1996. Does bigger mean better? Evolutionary determinants of brain size and structure. *Brain Behav. Evol.* **47**: 225–245.

Aiello, L.C. & Wheeler, P. 1995. The expensive-tissue hypothesis: the brain and the digestive-system in human and primate evolution. *Curr. Anthropol.* **36**: 199–221.

Alexander, R.D., Hoogland, J.L., Howard, R.D., Noonan, K.M. & Sherman, P.W. 1979. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. In: *Evolutionary Biology and Human Social Behaviour: An Anthropological Perspective* (N. Chagnon & W. Irons, eds), pp. 402–435. Duxbury Press, Duxbury, North Scituate, Massachusetts.

Allman, J. 2000. *Evolving Brains*. Scientific American Library, New York City, New York.

Allman, J., McLaughlin, T. & Hakeem, A. 1993. Brain weight and life-span in primate species. *Proc. Natl. Acad. Sci. U.S.A.* **90**: 118–122.

Amiel, J.J., Tingley, R. & Shine, R. 2011. Smart moves: effects of relative brain size on establishment success of invasive amphibians and reptiles. *PLoS ONE* **6**: e18277.

Arnould, J.P. & Duck, C.D. 1997. The cost and benefits of territorial tenure, and factors affecting mating success in male Antarctic fur seals. *J. Zool.* **241**: 649–664.

Bartholomew, G.A. 1970. A model for the evolution of pinniped polygyny. *Evolution* **24**: 546–559.

Bininda-Emonds, O.R.P. & Gittleman, J.L. 2000. Are pinnipeds functionally different from fissiped carnivores? The importance of phylogenetic comparative analyses. *Evolution* **54**: 1011–1023.

Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? *Q. Rev. Biol.* **75**: 385–407.

Byrne, R.W. & Whiten, A. 1997. Machiavellian intelligence. In: *Machiavellian Intelligence II. Extensions and Evaluations* (A. Whiten & R.W. Byrne, eds), pp. 1–23. Cambridge University Press, Cambridge, UK.

Clutton-Brock, T.H., Harvey, P.H. & Rudder, B. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature* **269**: 797–800.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*, 2 edn. John Murray, London.

Dechmann, D.K.N. & Safi, K. 2009. Comparative studies of brain evolution: a critical insight from the Chiroptera. *Biol. Rev.* **84**: 161–172.

Deutsch, C.J., Haley, M.P. & Le Boeuf, B.J. 1990. Reproductive effort of male northern elephant seals: estimates from mass loss. *Can. J. Zool.* **68**: 2580–2593.

Dunbar, R.I.M. 1998. The social brain hypothesis. *Evol. Anthropol.* **6**: 178–190.

Dunbar, R.I.M. & Shultz, S. 2007. Evolution in the social brain. *Science* **317**: 1344–1347.

Dunn, P.O., Whittingham, L.A. & Pitcher, T.E. 2001. Mating systems, sperm competition and the evolution of sexual dimorphism in birds. *Evolution* **55**: 161–175.

Fairbairn, D.J. 2007. The enigma of sexual size dimorphism. In: *Sex, Size, and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism* (D.J. Fairbairn, W.U. Blanckenhorn & T. Székely, eds), pp. 1–10. Oxford University Press, Oxford.

Ferguson, S.H. 2006. The influences of environment, mating habitat, and predation on evolution of pinniped lactation strategies. *J. Mamm. Evol.* **13**: 63–82.

Freckleton, R.P. 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J. Anim. Ecol.* **71**: 542–545.

Freckleton, R.P., Harvey, P.H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**: 712–726.

Garamszegi, L.Z., Eens, M., Erritzoe, J. & Møller, A.P. 2005. Sperm competition and sexually size dimorphic brains in birds. *Proc. R. Soc. B* **272**: 159–166.

García-Berthou, E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *J. Anim. Ecol.* **70**: 708–711.

González-Lagos, C., Sol, D. & Reader, S.M. 2010. Large-brained mammals live longer. *J. Evol. Biol.* **23**: 1064–1074.

Gonzalez-Voyer, A. & Kolm, N. 2009. Distinct evolutionary patterns of brain and body size during adaptive radiation. *Evolution* **63**: 2266–2274.

Gonzalez-Voyer, A. & Kolm, N. 2010. Sex, ecology and the brain: evolutionary correlates of brain structure volumes in Tanganyikan cichlids. *PLoS ONE* **5**: e14355.

Gonzalez-Voyer, A., Fitzpatrick, J.L. & Kolm, N. 2008. Sexual selection governs parental care patterns in cichlid fish. *Evolution* **62**: 2015–2026.

Gonzalez-Voyer, A., Winberg, S. & Kolm, N. 2009. Brain structure evolution in a basal vertebrate clade: evidence from phylogenetic comparative analysis of cichlid fishes. *BMC Evol. Biol.* **9**: 238.

Guay, P.J. & Iwaniuk, A.N. 2008. Interspecific variation in relative brain size is not correlated with intensity of sexual selection in waterfowl (Anseriformes). *Aust. J. Zool.* **56**: 311–321.

Healy, S.D. & Rowe, C. 2007. A critique of comparative studies of brain size. *Proc. R. Soc. B* **274**: 453–469.

Higdon, J.W., Bininda-Emonds, O.R.P., Beck, R.M.D. & Ferguson, S.H. 2007. Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset. *BMC Evol. Biol.* **7**: 216.

Hutcheon, J.M., Kirsch, J.W. & Garland, T. 2002. A comparative analysis of brain size in relation to foraging ecology and phylogeny in the chiroptera. *Brain Behav. Evol.* **60**: 165–180.

Isler, K. & van Schaik, C.P. 2006a. Costs of encephalization: the energy trade-off hypothesis tested on birds. *J. Hum. Evol.* **51**: 228–243.

Isler, K. & van Schaik, C.P. 2006b. Metabolic costs of brain size evolution. *Biol. Lett.* **2**: 557–560.

Jacobs, L.F. 1996. Sexual selection and the brain. *Trends Ecol. Evol.* **11**: 82–86.

Jerison, H.J. 1973. *Evolution of the Brain and Intelligence*. Academic Press, New York City, New York.

Jerison, H.J. 1991. *Brain Size and the Evolution of Mind*. American Museum of Natural History, New York City, New York.

Jones, K.E. & MacLarnon, A. 2004. Affording larger brains: testing hypotheses of mammalian brain evolution in bats. *Am. Nat.* **164**: E20–E31.

Kaufman, J.A. 2003. On the expensive-tissue hypothesis: independent support from highly encephalized fish. *Curr. Anthropol.* **44**: 705–706.

Kotrschal, K., Van Staaden, M.J. & Huber, R. 1998. Fish brains: evolution and environmental relationships. *Rev. Fish Biol. Fisheries* **8**: 373–408.

Kovacs, K.M. & Lavigne, D.M. 1986. Maternal investment and neonatal growth in phocid seals. *J. Anim. Ecol.* **55**: 1035–1051.

Kovacs, K.M. & Lavigne, D.M. 1992. Maternal investment in otariid seals and walruses. *Can. J. Zool.* **70**: 1953–1964.

Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution* **33**: 402–416.

Lefebvre, L., Reader, S.M. & Sol, D. 2004. Brains, innovations and evolution in birds and primates. *Brain Behav. Evol.* **63**: 233–246.

Lemaître, J.-F., Ramm, S.A., Barton, R.A. & Stockley, P. 2009. Sperm competition and brain size evolution in mammals. *J. Evol. Biol.* **22**: 2215–2221.

Lindenfors, P., Tullberg, B.S. & Biuw, M. 2002. Phylogenetic analysis of sexual selection and sexual size dimorphism. *Behav. Ecol. Sociobiol.* **52**: 188–193.

Lindenfors, P., Nunn, C.L. & Barton, R.A. 2007. Primate brain architecture and selection in relation to sex. *BMC Biol.* **5**: 20.

Lindstedt, S.L. & Boyce, M.S. 1985. Seasonality, fasting endurance, and body size in mammals. *Am. Nat.* **125**: 873–878.

Maddison, W.P. & Maddison, D.R. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org.

Maklakov, A.A., Immler, S., Gonzalez-Voyer, A., Rönn, J. & Kolm, N. 2011. Brains and the city: big brained passerine birds succeed in urban environments. *Biol. Lett.* **7**: 730–732.

Mardia, K.V., Kent, J.T. & Bibby, J.M. 1979. *Multivariate Analysis*. Academic Press, London.

Marino, L., Sol, D., Thoren, K. & Lefebvre, L. 2006. Does diving limit brain size in cetaceans? *Mar. Mamm. Sci.* **22**: 413–425.

Martin, R.D. 1996. Scaling of the mammalian brain: the maternal energy hypothesis. *News Physiol. Sci.* **11**: 149–156.

McCann, T.S. 1981. Aggression and sexual activity of male Southern elephant seals, Mirounga leonina. *J. Zool.* **195**: 295–310.

Modig, A.O. 1996. Effect of body size and harem size on male reproductive behaviour in the southern elephant seal. *Anim. Behav.* **51**: 1295–1306.

Navarrete, A., van Schaik, C.P. & Isler, K. 2011. Energetics and the evolution of human brain size. *Nature* **480**: 91–93.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.

Pitnick, S., Jones, K.E. & Wilkinson, G.S. 2006. Mating system and brain size in bats. *Proc. R. Soc. B* **273**: 719–724.

R Development Core Team 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. http://www.R-project.org.

Reader, S.M. & Laland, K.N. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl. Acad. Sci. U.S.A.* **99**: 4436–4441.

Revell, L.J. 2009. Size-correction and principal components for interspecific comparative studies. *Evolution* **63**: 3258–3268.

Robin, E.D. 1973. The evolutionary advantages of being stupid. *Perspect. Biol. Med.* **16**: 369–379.

Schulz, T.M. & Bowen, W.D. 2004. Pinniped lactation strategies: evaluation of data on maternal and offspring life history traits. *Mar. Mamm. Sci.* **20**: 86–114.

Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P. & Lefebvre, L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl. Acad. Sci. U.S.A.* **102**: 5460–5465.

Sol, D., Székely, T., Liker, A. & Lefebvre, L. 2007. Big-brained birds survive better in nature. *Proc. R. Soc. B* **274**: 763–769.

Sol, D., Bacher, S., Reader, S.M. & Lefebvre, L. 2008. Brain size predicts the success of mammal species introduced into novel environments. *Am. Nat.* **172**: S63–S71.

Striedter, G.F. 2005. *Principles of Brain Evolution*. Sinauer Associates Inc., Sunderland, Massachusetts.

Thomas, G.H. & Freckleton, R.P. 2012. MOTMOT: models of trait macroevolution on trees. *Methods Ecol. Evol.* **3**: 145–151.

Thomas, G.H., Meiri, S. & Phillimore, A.B. 2009. Body size diversification in *Anolis*: novel environment and island effects. *Evolution* **63**: 2017–2030.

Tinker, M.T., Kovacs, K.M. & Hammill, M.O. 1995. The reproductive behavior and energetics of male grey seals (*Halichoerus grypus*) breeding on a land-fast ice substrate. *Behav. Ecol. Sociobiol.* **36**: 159–170.

Webster, M.S. 1992. Sexual dimorphism, mating system and body size in New World Blackbirds (Icterinae). *Evolution* **46**: 1621–1641.

Worthy, G.A.J. & Hickie, J.P. 1986. Relative brain size in marine mammals. *Am. Nat.* **128**: 445–459.

Supporting Information

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

Figure S1 Maximum likelihood reconstruction of the degree of sexual selection in pinnipeds.

Table S1 Multiple regressions models of brain mass in relation to body mass and various predictor variables for males and females when controlling for phylogeny (PGLS).

Table S2 Species trait data for extant pinnipeds used in this study.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.