

## Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation

Martín-Alejandro Serrano-Meneses and Tamás Székely

Serrano-Meneses, M. A. and Székely, T. 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. – *Oikos* 113: 385–394.

Seabirds exhibit a range of sexual size dimorphism (SSD) that includes both male-biased (males > females) and female-biased SSD (males < females). Here we use phylogenetic comparative methods to test the selective processes that may influence their SSD. Using phylogenetically independent contrasts we show that the sizes of males and females are scaled isometrically in seabirds. We also test three functional hypotheses of SSD: sexual selection, fecundity selection and differential niche-utilisation. First, we found support for the sexual selection hypothesis, even though seabirds are socially monogamous and, as a consequence one might expect sexual selection to be weak. We show that SSD is correlated with an aspect of sexual selection, the agility of male displays, since in species that exhibit aerial displays the males are smaller (relative to the female) than in species in which the males display on the ground. Second, our results are not consistent with the fecundity selection hypothesis, since contrary to the predicted trend, female seabirds lay larger eggs in male-biased species than in female-biased ones. Finally, our results are not consistent with a previous study of the differential niche-utilisation hypothesis, since we found no relationship between SSD and ocean primary productivity in the breeding areas. Taken together, we suggest that seabird SSD is most consistent with the sexual selection hypothesis via the agility of male displays. Nevertheless, further data and tests are required to establish whether different resource utilisation by males and females may also select for SSD.

*M. A. Serrano-Meneses and T. Székely, Dept of Biology and Biochemistry, Univ. of Bath, UK, BA2 7AY (bspmasm@bath.ac.uk).*

A difference in body size between males and females, sexual size dimorphism (SSD), is a prevailing characteristic in a wide range of animal taxa (Andersson 1994, Fairbairn 1997, Blanckenhorn 2000). Three major processes have been proposed that produce and maintain SSD (reviewed by Jehl and Murray 1986, Hedrick and Temeles 1989, Andersson 1994). First, Darwin (1871) noted that if sexual selection is more intense in one sex than in the other (either via male–male competition or female choice) then SSD is likely to emerge (Payne 1984, Webster 1992, Owens and Hartley 1998). The direction of sexual selection on body size, however, may depend on whether the competition occurs on the ground or in the

air (Payne 1984, Jehl and Murray 1986, Figuerola 1999, Székely et al. 2004). For instance, sexual selection is expected to favour small body size in males that exhibit aerial displays (Andersson and Norberg 1981, Hakkarainen et al. 1996, Blomqvist et al. 1997, Székely et al. 2000), whereas if males display or fight on the ground, then large size is often advantageous (Clutton-Brock et al. 1982, Anderson and Fedak 1985, Lindenfors and Tullberg 1998, Székely et al. 2000, Lindenfors et al. 2002).

Second, fecundity selection for large size has been proposed to explain female-biased SSD in many invertebrates, fish and birds (Andersson 1994). The optimal

---

Accepted 15 September 2005  
Subject Editor: Jan Lindström

Copyright © OIKOS 2006  
ISSN 0030-1299

body size may differ between the sexes if large females have higher reproductive success due to their higher capacity for laying eggs (Ridley and Thompson 1979, Wiewandt 1982, Honěk 1993), or if males prefer large females to small ones (Sandercock 1998, 2001). Consistently, studies of spiders, insects and ectotherm vertebrates, such as fishes and frogs, have demonstrated positive relationships between female body size and fecundity (Shine 1979, Head 1995, Prenter et al. 1999).

Third, males and females may have different body sizes to avoid resource–competition, or enhance feeding efficiency (differential niche-utilisation, Selander 1966, Shine 1989, Thom et al. 2004). Since body size or morphology is often evolved to adapt to different niches (Shine 1989, Sandercock 2001), sexually dimorphic pairs can exploit a wider range of resources than monomorphic ones (Figuerola 1999).

A puzzling allometric relationship exists between body size and sexual size dimorphism in many animals: in taxa with male-biased dimorphism SSD increases with body size, whereas the extent of female-biased SSD decreases with body size (Rensch's rule, Abouheif and Fairbairn 1997, Fairbairn 1997). Several hypotheses have been suggested to explain Rensch's rule, and a recent comparative study showed that the Rensch's rule was most consistent with selection pressures emerging from two aspects of sexual selection: intensity of male–male competition and agility of male displays (Székely et al. 2004).

Seabirds (bird taxa living in and making their living from marine environments; 193 species, Monroe and Sibley 1993, Diomedinae, Fregatidae, Hydrobatinae, Pelecaninae, Phaethontidae, Phalacrocoracidae, Procellariinae, Spheniscidae and Sulidae, excluding the super-families Ardeioidea, Ciconiidea, Phoenicopterioidea, Scopoidea, Threskiornithoidea the family Anhingidae and the sub-family Balaenicipitinae) are excellent organisms to investigate functional hypotheses of SSD, since they exhibit both male-biased and female-biased dimorphisms. A previous study found that seabirds in more productive areas exhibited male-biased SSD (Fairbairn and Shine 1993), and showed that seabirds exhibited SSD consistent with Rensch's rule. Fairbairn and Shine (1993) however, only used Southern Hemisphere species, and investigated the putative explanatory variables mostly in isolation from each other. Furthermore, Fairbairn and Shine (1993) did not investigate the influence of sexual selection on SSD, since all seabirds are socially monogamous. Nevertheless, sexual selection may still influence SSD in monogamous species via selecting for agility (and thus small size) in males (Jehl and Murray 1986, Figuerola 1999, Székely et al. 2000).

Here we first test whether seabirds exhibit Rensch's rule using species from both Northern and Southern Hemispheres. Second, we test three functional hypotheses of SSD: (i) if sexual selection influences SSD, we

expected to find a relationship between agility of male displays and SSD: male-biased SSD should occur with non-agile displays. (ii) If fecundity selection influences female size, then both egg size and clutch size should increase with the size of female relative to male. (iii) If differential niche-utilisation of resources influences SSD, following Fairbairn and Shine (1993) we predict that differences between female and male size should be more pronounced in those species that breed in areas of low ocean primary productivity, because the male and the female of a breeding pair should specialise in exploiting different resources to avoid food competition. Conversely, those species that have highly productive feeding areas around their breeding site should be monomorphic.

## Methods

### Data

We collected data on body mass, clutch size and egg size, and descriptions of male display behaviour from published sources (handbooks and reference books; Appendix 1). We used those seabird taxa for which body mass data were available. We also recorded the geographic location of the breeding site where the morphometric measures were taken to derive the ocean primary productivity. Male displays were scored blindly to the identity of species by three observers using the descriptions of male displays as follows: (1) ground display; (2) both ground and aerial displays: males displayed from nests or territories but also engaged in aerial activities such as the stealing of nest material from other nests; (3) aerial display: males displayed acrobatically or non-acrobatically in the air (see similar approach by Figuerola 1999 and Székely et al. 2000; Appendix 1). The correlations between the scores of three observers were high (all Spearman's rank correlation coefficients  $r_s > 0.883$ ,  $p = 0.001$ ,  $n = 71$ ).

Ocean productivity was derived from a composite map of September 1998 – August 1999 (SEAWIFS: estimated primary productivity map, [http://marine.rutgers.edu/opp/swf/Production/results/all2\\_swf.html](http://marine.rutgers.edu/opp/swf/Production/results/all2_swf.html)). Ocean primary productivity was estimated from visible light reflectance using the consensus algorithm for chlorophyll concentration (Behrenfeld and Falkowski 1997). We calibrated this map such that the value of each pixel (every pixel measures approximately 18 km per side, i.e. 324 km<sup>2</sup>) corresponded to the chlorophyll concentration (grams of carbon m<sup>-2</sup>) by plotting the palette order of pixels in the colour-scale of the map against chlorophyll concentration to obtain the relationship  $OP = 0.5556/\text{palette order}$ . This was applied as an image calculation using the image software Idrisi 3.32 (Clark Labs: <http://www.clarklabs.org>). At each breeding location, ocean productivity was measured in 16 surrounding pixels

(within an estimated area of 5184 km<sup>2</sup>). For those breeding locations where information was not available (i.e. Antarctica), we estimated the OP at the closest breeding location. The average ocean production of 16 pixels was used in the analyses, with a minimum value of productivity of 56 and a maximum of 450 g of carbon m<sup>-2</sup>.

## Phylogeny

We used a composite phylogeny of seabirds (5 families, 4 sub-families, 73 species; Fig. 1) by augmenting the

DNA–DNA hybridisation phylogeny of Sibley and Ahlquist (1990; Fig. 366–368) with recent molecular phylogenies. Where possible, we included changes in the existing phylogeny if supported by new molecular evidence. Thus, Diomedeinae, Procellariinae, Hydrobatinae and Spheniscidae were taken from Nunn and Stanley (1998), Fregatidae was taken from Kennedy and Spencer (2004), Pelecaninae was taken from Sibley and Ahlquist (1990; Fig. 367), Sulidae was taken from Friesen and Anderson (1997) and Phalacrocoracidae was taken from on Kennedy et al. (2000). To see whether our results were sensitive to the phylogenetic hypothesis, we

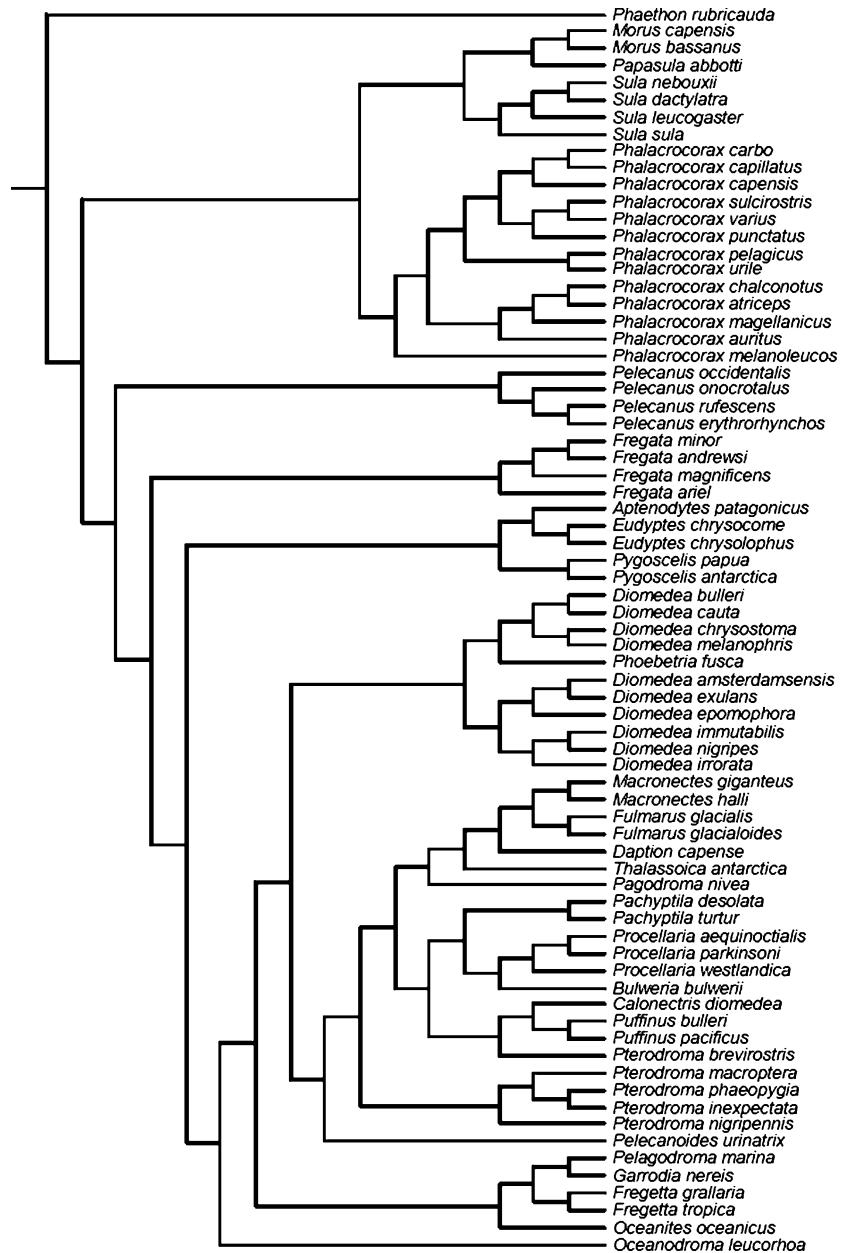


Fig. 1. Composite seabird phylogeny composed of Sibley and Ahlquist's (1990) UPGMA tree with molecular phylogenies of individual seabird families.

reanalysed our data using Kennedy and Page (2002) seabird supertree. Since Kennedy and Page (2002) do not include *Pterodroma brevirostris* in their supertree, this species was not included in our re-analyses.

Phylogenetic analyses with Kennedy and Page (2002) were largely consistent with our main results; here we only provide those that are qualitatively different.

## Phylogenetic analyses

We used the phylogenetic independent contrasts method of Felsenstein (1985) as implemented by CAIC (Purvis and Rambaut 1995) to control for phylogenetic non-independence of species (Harvey and Pagel 1991). An assumption of Felsenstein's method (1985) is that the standardized contrasts should be independent from their estimated nodal values: the distributions of our data were consistent with this assumption. All branch lengths were set to equal values.

We tested Rensch's rule by fitting a major axis regression (model II regression, Sokal and Rohlf 1981) through the origin using phylogenetic independent contrasts (Harvey and Pagel 1991, Garland et al. 1992). We provide the slopes of these regressions and their 95% confidence intervals (lower CI – upper CI). Slopes and confidence intervals of major axis regressions were calculated by bootstrapping the contrasts using R (R Development Core Team, <http://www.R-project.org>).

Data were  $\log_{10}$  transformed prior to the analyses, except display scores. SSD was calculated as contrasts in  $\log_{10}$  (male body mass) – contrasts in  $\log_{10}$  (female body mass). Log transformed data are commonly used to calculate SSD. The difference between male and female size expressed as a logarithm is more accurate than ratios because ratios have undesired statistical properties (Smith 1999). Egg size (in  $\text{mm}^3$ ) was estimated by calculating the egg-index ( $\text{egg-length} \times \text{breadth}^2$ ).

We tested functional hypotheses of SSD by investigating the relationship between SSD (dependent variable) and explanatory variables (display behaviour, clutch size and egg size, and ocean productivity) in bivariate and multivariate least squares regressions. These regressions were forced through the origin (Harvey and Pagel 1991), and when appropriate, we provide partial correlation coefficients. We also tested whether absolute SSD was related to ocean productivity since the differential niche-utilisation hypothesis does not make a priori assumption on the direction of SSD. Therefore, we performed a bivariate regression using the absolute values of contrasts in SSD (dependent variable) and contrasts in ocean productivity (independent variable). We constructed a multivariate model that initially included all four hypothesised explanatory variables (display behaviour, clutch size, egg size, ocean productivity), and then used backward elimination to remove non-significant

variable(s). Then the influences of all pairwise statistical interactions of the initial model were tested on SSD, however, only the effect of clutch size  $\times$  egg size was marginally significant ( $p = 0.068$ ). Since clutch size and egg size had similar effects on SSD in regards to sign and magnitude, this interaction was not considered further.

Statistical calculations were carried out using SPSS (Ver. 11) and Minitab (release 12).

## Results

### Distribution of SSD among seabird families

Seabirds exhibit both male- and female-biased SSDs, and the median SSD is significantly different among families (Fig. 2, Kruskal–Wallis  $H = 46.482$ ,  $df = 8$ ,  $p = 0.0001$ ). Males are larger than females in Diomedeiinae (Wilcoxon one-sample tests,  $W = 66$ ,  $p = 0.004$ ,  $n = 11$ ), Phalacrocoracidae ( $W = 91$ ,  $p = 0.002$ ,  $n = 13$ ), Procellariinae ( $W = 233$ ,  $p = 0.001$ ,  $n = 22$ ), Pelecaninae ( $W = 10$ ,  $p = 0.1$ ,  $n = 4$ ) and Spheniscidae ( $W = 13$ ,  $p = 0.178$ ,  $n = 5$ ) although the trend in the latter two groups is not supported statistically. Also, there is a strong, but statistically non-significant female-biased SSD in Sulidae ( $W = 2$ ,  $p = 0.052$ ,  $n = 7$ ), Fregatidae ( $W = 0$ ,  $p = 0.1$ ,  $n = 4$ ), and Hydrobatinae ( $W = 0$ ,  $p = 0.059$ ,  $n = 6$ ). SSD in Phaethontidae ( $W = 0$ ,  $p = 1$ ,  $n = 1$ ) is not different from unity.

### Rensch's rule

At species level, seabirds exhibit the Rensch's rule since the slope of major axis regression ( $b = 1.037$ ,  $n = 73$  species) is greater than one (lower 95% CI – upper 95% CI: 1.015–1.060,  $n = 73$  species). However, the results of

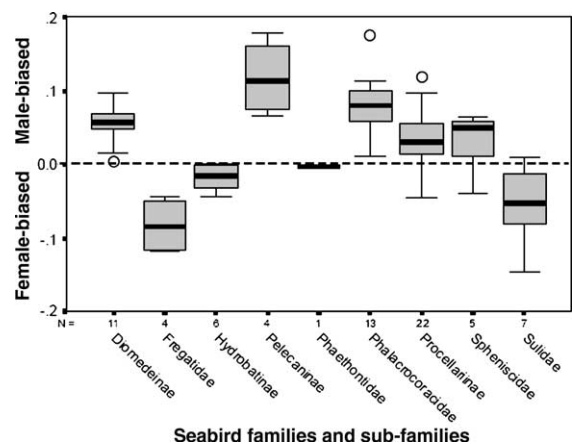


Fig. 2. Sexual size dimorphism in body mass of seabird families and sub-families (median, lower and upper quartiles; whiskers are extremes). N denotes the number of species in each family (or sub-family), and the dotted line represents monomorphism.

major axis regression using phylogenetically independent contrasts is not consistent with the species-level result, since the confidence intervals include the isometric relationship ( $b = 1.044$ ,  $0.929-1.067$ ,  $n = 72$  contrasts; Fig. 3). The latter result remains consistent when one outlier data point was excluded from the analysis (data point 'A' in Fig. 3,  $b = 1.054$ ,  $0.999-1.088$ ,  $n = 71$  contrasts). The data point was excluded under the rationale that one single outlier may bias the results. However, using the alternative supertree of Kennedy and Page (2002), we found weak support for Rensch's rule ( $b = 1.056$ ,  $1.010-1.079$ ,  $n = 68$  contrasts).

### Sexual selection, fecundity selection and differential niche-utilisation

Evolutionary increases in male display agility correlated with evolutionary changes toward female-biased SSD ( $r = -0.233$ ,  $p = 0.050$ ,  $n = 70$  contrasts, Fig. 4). Since display contrasts were highly variable around zero, we repeated the latter analysis by excluding them from the bivariate regression (see similar approach by Owens and Hartley 1998). The relationship between SSD and display remained significant ( $r = -0.325$ ,  $p = 0.030$ ,  $n = 44$  contrasts). Furthermore, by excluding an outlier (data point 'B' in Fig. 4) the relationship became stronger ( $r = -0.338$ ,  $p = 0.025$ ,  $n = 43$ ).

Both measures of fecundity were related to SSD ( $r^2 = 0.129$ ,  $p = 0.011$ ,  $n = 66$  contrasts; clutch size, partial  $r = 0.253$ ,  $p = 0.035$ ; egg size, partial  $r = 0.306$ ,  $p = 0.010$ ). Thus, evolutionary increases toward large males relative to females were associated with increases in both clutch size and egg size. Note that these relationships are the opposite of the predicted ones:

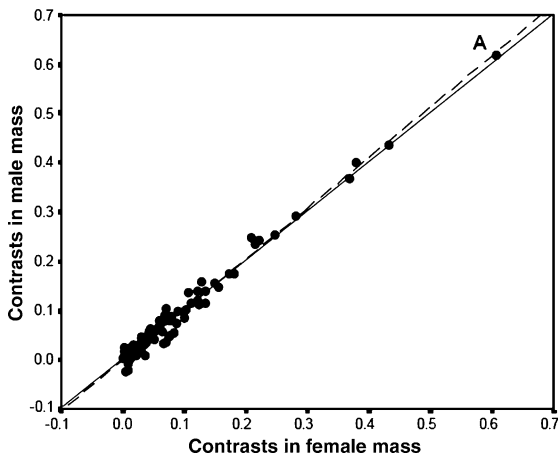


Fig. 3. The relationship between independent contrasts of  $\log_{10}$ (male body mass) and  $\log_{10}$ (female body mass). The continuous line indicates the isometric relationship, and the dotted line represents the fitted relationship using major axis regression through zero ( $b = 1.044$ ,  $n = 72$  contrasts).

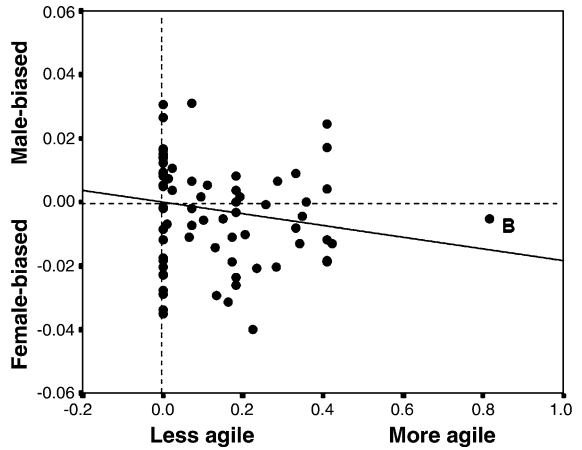


Fig. 4. Phylogenetically independent contrasts in sexual size dimorphism (SSD) and male display agility ( $r = -0.233$ ,  $p = 0.050$ ,  $n = 70$  contrasts). Regression was forced through the origin.

since increases in clutch and egg size were expected to increase with large female size relative to males.

Ocean productivity was not related to SSD, since there was no relationship between SSD and the ocean productivity around the breeding areas ( $r = 0.0001$ ,  $p = 0.903$ ,  $n = 72$  contrasts). Similarly, when we tested for the relationship between absolute values of SSD and ocean productivity ( $r = 0.004$ ,  $p = 0.975$ ,  $n = 72$ ), no relationship was found.

These results are consistent with the full multivariate model, since ocean productivity was not retained in the final model, whereas egg size remained correlated with SSD, and clutch size and display behaviour were marginally significant (Table 1). Note, that the direction of relationships between SSD, clutch size and egg size remained inconsistent with the fecundity hypothesis.

### Discussion

Our study provided four major results. First, at species level, seabirds appear to follow Rensch's rule, however, this relationship no longer holds when we use the phylogenetically independent contrasts using composite phylogeny. Note, however, that once an outlier value was excluded from the analyses, the results were near to significance. Also, when we use Kennedy and Page (2002) seabird supertree we find weak support for Rensch's rule. Thus, seabirds, unlike shorebirds, hummingbirds and bustards (Colwell 2000, Raihani et al. 2006), Rensch's rule does only exist as a trend but we conclude that it is not statistically significant. In shorebirds, Székely et al. (2004) proposed that the intensity of sexual selection and the agility of male displays influenced the evolution (or maintenance) of Rensch's rule. Their findings are consistent with our work, since

Table 1. Final multivariate model using phylogenetic independent contrasts. The dependent variable is contrasts in  $\log_{10}$ (male body mass) – contrasts in  $\log_{10}$ (female body mass) ( $r^2 = 0.170$ ,  $n = 69$  contrasts).

Independent variables	Slope $\pm$ SE	Partial correlation coefficient	p
Clutch size	0.09718 $\pm$ 0.050	0.235	0.054
Egg size	0.05200 $\pm$ 0.020	0.300	0.013
Display behaviour	-0.01541 $\pm$ 0.009	-0.214	0.080

seabirds are socially monogamous whereas shorebirds also exhibit social polygamy; therefore sexual selection in seabirds appears to be less intense than in shorebirds. Note that various other hypotheses outlined by Fairbairn (1997) remained untested by both Székely et al. (2004) and us.

Second, male agility correlated with SSD. Thus sexual selection, in the form of male display behaviour, appears to influence SSD in seabirds. In this work we use a paraphyletic group (seabirds), so one potential criticism is that the inclusion or exclusion of related taxa might change our results. However, we believe that this is unlikely because we do not use ancestral states to perform directional analyses as we are interested in the phylogenetic independence of the taxa. Males tend to be larger, relative to females in those species where males display on the ground, whereas selection appears to favour small male size in those species that exhibit aerial display. The effect of male display behaviour was moderate, although we should bear in mind that agility, as represented by the scores, was a crude variable. Nevertheless, strong ecological constraints (viability selection, Blanckenhorn 2000) and low levels of mating competition (all seabirds are socially monogamous) may restrain the sexes to similar sizes. Note, that correlational methods, such as phylogenetic independent contrasts, cannot separate cause and effect. Further comparative works using directional phylogenetic methods are thus needed (Pagel 1994).

Third, both clutch size and egg size correlate with SSD, however, these relationships are not consistent with the fecundity selection hypothesis. It is not obvious why SSD increases with egg size and clutch-size. One potential explanation is that males of all seabirds contribute to incubation and brood-rearing, so that increasing male size allows efficient incubation. On the other hand, it is possible that strong genetic correlation between male and female size may also have an indirect effect on egg and clutch size.

Fourth, unlike Fairbairn and Shine's (1993) study, ocean productivity was unrelated to SSD. The lack of relationship between their results and ours may be due to differences in ocean productivity data: Fairbairn and Shine estimated minimum levels for rates of primary production of the surrounding ocean in the breeding areas (rate of carbon fixation in  $\text{g m}^{-2}$ , to the nearest 50 g) using a global map with four possible levels of productivity (Löfgren 1984). In our study we calculated

ocean productivity from a map that estimated chlorophyll concentration (grams of carbon  $\text{m}^{-2}$ ) from visible light reflectance (SEAWIFS: Estimated Primary Productivity map, [http://marine.rutgers.edu/opp/swf/Production/results/all2\\_swf.html](http://marine.rutgers.edu/opp/swf/Production/results/all2_swf.html)) and with approximately 450 levels of productivity. On the one hand, using Fairbairn and Shine's species only, the correlation between our data on SSD and theirs is highly significant (mean SSD value from their populations,  $r = -0.925$ ,  $p = 0.001$ ,  $n = 37$ ); this strengthens the view that the two SSD datasets are comparable. On the other hand, Fairbairn and Shine's ocean productivity data were not correlated with our data on ocean productivity ( $r = -0.214$ ,  $p = 0.217$ ,  $n = 35$ ). Taken together, we conclude that the main difference between the results of Fairbairn and Shine and ours is due to the differences in ocean productivity data.

However, we argue that Fairbairn and Shine's own results do not support the differential niche-utilisation hypothesis. First, Fairbairn and Shine (1993) show that males tend to be larger than females in seabird populations (i) that have large average body mass and (ii) that breed in areas of high ocean productivity. This relationship, however, is the opposite of what may be predicted by the differential niche-utilisation hypothesis: more dimorphic taxa should be found in areas of low ocean productivity, whilst more monomorphic taxa should inhabit areas of high ocean productivity. Second, Fairbairn and Shine (1993) demonstrate that body size, SSD and Carbon fixation are tightly correlated and using multivariate analyses to separate highly correlated linear variables may not be relevant due to colinearity.

We conclude that sexual selection influences SSD in seabirds, although this influence appears to be weaker than that in several avian taxa such as shorebirds, bustards and North American blackbirds. Our results, however, do not support the fecundity selection and the differential niche-utilisation hypotheses. Further research should tease apart the correlates of male–male competition and female choice, use directional methods to separate cause and effect and provide better data for testing the differential niche-utilisation, for instance, by using direct estimates on the availability of prey species around feeding areas throughout the year and information on sex specific feeding strategies.

*Acknowledgements* – We thank Zoltan Barta (Univ. of Debrecen) for writing the R code to calculate the major axis regression through zero and Peter Long for helping in the calculation of ocean productivity. We also thank Hugh

Drummond, Jessica Pollitt and Gavin Thomas for scoring male agility. Gina Raihani and Gavin Thomas provided valuable comments on an earlier version of this manuscript. MASM was supported by CONACYT (Reg. 168893) and Hospital Guillermo González Cervantes, Mexico.

## References

- Abouheif, E. and Fairbairn, D. J. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's Rule. – *Am. Nat.* 149: 540–562.
- Anderson, S. S. and Fedak, M. F. 1985. Grey seal males: energetic and behavioural links between size and sexual success. – *Anim. Behav.* 33: 829–838.
- Andersson, M. 1994. Sexual selection. – Princeton Univ. Press.
- Andersson, M. and Norberg, R. A. 1981. Evolution of reversed sexual size dimorphism and role partitioning among raptors, with a size scaling of flight performance. – *Biol. J. Linn. Soc.* 15: 105–130.
- Behrenfeld, M. J. and Falkowski, P. G. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. – *Limnol. Oceanogr.* 42: 1–20.
- Blanckenhorn, W. U. 2000. The evolution of body size: what keeps organisms small? – *Q. Rev. Biol.* 75: 385–407.
- Blomqvist, D., Johansson, O.C., Unger, U. et al. 1997. Male aerial display and reversed sexual size dimorphism in the dunlin. – *Anim. Behav.* 54: 1291–1299.
- Causey, D. 2002. Red-faced cormorant (*Phalacrocorax urile*). – In: Poole, A. and Gill, F. (eds), *The birds of North America*. No. 617. Acad. Natl. Sci. Am. Ornithol. Union.
- Clark Labs, <http://www.clarklabs.org>
- Clutton-Brock, T. H., Guinness, F. E. and Albon, S. D. 1982. Red deer: behavior and ecology of two sexes. – Univ. of Chicago Press.
- Colwell, R. K. 2000. Rensch's rule crosses the line: convergent allometry of sexual size dimorphism in hummingbirds and flower mites. – *Am. Nat.* 156: 495–510.
- Cramp, S. and Simmons, K. E. L. 1977. *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palaearctic*. Vol. 1. – Oxford Univ. Press.
- Cushman-Murphy, R. and Pennoyer, J. M. 1952. Larger petrels of the genus *Pterodroma*. – *Am. Mus. Novitates*, No. 1580.
- Darwin, C. 1871. The descent of man and selection in relation to sex. – Princeton Univ. Press.
- Diamond, A. W. and Schreiber, E. A. 2002. Magnificent frigatebird (*Fregata magnificens*). – In: Poole, A. and Gill, F. (eds), *The birds of North America*. No. 601. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union.
- Dunning, J. B., Jr. 1983. *CRC handbook of avian body masses*. – CRC Press.
- Evans, R. M. and Knopf, F. L. 1993. American white pelican (*Pelecanus erythrorhynchos*). – In: Poole, A. and Gill, F. (eds), *The birds of North America*. No. 57. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union.
- Fairbairn, J. and Shine, R. 1993. Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. – *Oikos* 68: 139–145.
- Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. – *Annu. Rev. Ecol. Syst.* 28: 659–687.
- Felsenstein, J. 1985. Phylogenies and the comparative method. – *Am. Nat.* 125: 1–15.
- Figuerola, J. 1999. A comparative study on the evolution of reversed size dimorphism in monogamous waders. – *Biol. J. Linn. Soc.* 67: 1–18.
- Fleet, R. R. 1974. The red-tailed tropicbird on Kure Atoll. – *Ornithol. Monogr.* 16: 1–64.
- Friesen, V. L. and Anderson, D. J. 1997. Phylogeny and evolution of the Sulidae (Aves: Pelecaniformes): a test of alternative modes of speciation. – *Mol. Phyl. Evol.* 7: 252–260.
- Garland, T. Jr., Harvey, P. H. and Ives, A. R. 1992. Procedures for the analyses of comparative data using phylogenetically independent contrasts. – *Syst. Biol.* 41: 18–32.
- Gauger-Metz, V. and Schreiber, E. A. 2002. Great frigatebird (*Fregata minor*). – In: Poole, A. and Gill, F. (eds), *The birds of North America*. No. 681. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union.
- Gould, P. J., King, W. B. and Sanger, G. A. 1974. Red-tailed tropicbird (*Phaethon rubricauda*). – In: King, W. B. (ed.), *Pelagic studies of seabirds in the central and eastern Pacific*: 206–231. Smithsonian Inst.
- Hakkaraianen, H., Huhta, E., Lahti, K. et al. 1996. A test of male mating and hunting success in the kestrel: the advantages of smallness? – *Behav. Ecol. Sociobiol.* 39: 375–380.
- Harris, M. P. 1970. The biology of an endangered species, the dark-rumped petrel (*Pterodroma phaeopygia*), in the Galápagos Islands. – *Condor* 72: 76–84.
- Harvey, P. and Pagel, M. D. 1991. *The comparative method in evolutionary biology*. – Oxford Univ. Press.
- Hatch, S. A. and Nettleship, D. N. 1998. Northern fulmar (*Fulmarus glacialis*). – In: Poole, A. and Gill, F. (eds), *The birds of North America*. No. 361. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union.
- Head, G. 1995. Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (Class Araneae). – *Evolution* 49: 776–781.
- Hedrick, A. V. and Temeles, E. J. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. – *Trends Ecol. Evol.* 4: 136–138.
- Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. – *Oikos* 66: 483–492.
- del Hoyo, J., Elliott, A. and Sargatal, J. 1992. *Handbook of the birds of the World*. Vol. 1. – Lynx Edicions, Barcelona.
- Huntington, C. E., Butler, R. G. and Mauck, R. A. 1996. Leach's storm-petrel (*Oceanodroma leucorhoa*). – In: Poole, A. and Gill, F. (eds), *The birds of North America*. No. 233. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union.
- Imber, M. J. 1976. Breegind biology of the grey-faced petrel *Pterodroma macroptera gouldi*. – *N. Z. Dept of Internal Affairs Wildlife Publ.* 183: 51–64.
- Jehl Jr., J. R. and Murray Jr., B. G. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. – *Curr. Ornithol.* 3: 1–86.
- Jeremy, J. H. and Weseloh, D. V. 1999. Double-crested cormorant (*Phalacrocorax auritus*). – In: Poole, A. and Gill, F. (eds), *The birds of North America*. No. 441. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union.
- Johnsgard, P. A. 1993. *Cormorants, darters and pelicans of the World*. – Smithsonian Inst. Press.
- Jouventin, P. and Bried, J. 2001. The effect of mate choice on speciation in snow petrels. – *Anim. Behav.* 62: 123–132.
- Jouventin, P., Lequette, B. and Dobson, F. S. 1999. Age-related mate choice in the wandering albatross. – *Anim. Behav.* 57: 1099–1106.
- Kennedy, M. and Page, R. D. M. 2002. Seabird supertrees: combining partial estimates of procellariiform phylogeny. – *Auk* 119: 88–108.
- Kennedy, M. and Spencer, H. G. 2004. Phylogenies of the frigatebirds (Fregatidae) and tropicbirds (Phaethonidae), two divergent groups of the traditional order Pelecaniformes, inferred from mitochondrial DNA sequences. – *Mol. Phyl. Evol.* 31: 31–38.
- Kennedy, M., Gray, R. D. and Spencer, H. G. 2000. The phylogenetic relationships of the shags and cormorants: can sequence data resolve a disagreement between behavior and morphology? – *Mol. Phyl. Evol.* 3: 345–359.
- Lindfors, P. and Tullberg, B. S. 1998. Phylogenetic analyses of primate size evolution: the consequences of sexual selection. – *Biol. J. Linn. Soc.* 64: 413–447.

- Lindenfors, P., Tullberg, B. S. and Biuw, M. 2002. Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. – *Behav. Ecol. Sociobiol.* 52: 188–193.
- Löfgren, L. 1984. Ocean birds: their breeding, biology and behaviour. – Croom and Helm, Canberra.
- Marchant, S. and Higgins, P. J. 1990. Handbook of Australian, New Zealand and Antarctic birds. – Vol. 1, Parts A and B. Oxford Univ. Press.
- Megyesi, J. L. and O'Daniel, D. 1997. Bulwer's petrel (*Bulweria bulwerii*). – In: The birds of North America. No. 281. Acad. Natl. Sci., Washington, DC: Am. Ornithol. Union.
- Metz, V. G. and Schreiber, E. A. 2002. Great frigatebird (*Fregata minor*). – In: Poole, A. and Gill, F. (eds), The birds of North America. No. 681. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union.
- Monroe, B. L. Jr. and Sibley, C. G. 1993. A World checklist of birds. – Yale Univ. Press.
- Nelson, B. 1978. The Sulidae: gannets and boobies. – Oxford Univ. Press.
- Nelson, B. 2002. The Atlantic gannet. – Biddles the Printers, Guildford.
- Norman, F. I. and Brown, R. S. 1987. Notes on common diving-petrels *Pelecanooides urinatrix* Found Beach-washed in Victoria, 1985. – *Emu* 87: 179–185.
- Nunn, G. B. and Stanley, S. E. 1998. Body size effects and rates of cytochrome b evolution in tube-nosed seabirds. – *Mol. Biol. Evol.* 15: 1360–1371.
- Owens, I.P.F. and Hartley, I.R. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? – *Proc. R. Soc. B* 265: 397–407.
- Pagel, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. – *Proc. R. Soc. B* 255: 37–45.
- Payne, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. – *J. Field Ornithol.* 56: 92–93.
- Prenter, J., Elwood, R. W. and Montgomery, W. I. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. – *Evolution* 53: 1987–1994.
- Provincial Museum of Alberta, the blue-footed booby, <http://www.pma.edmonton.ab.ca/vexhibit/eggs/vexeggs/wrldeggs/bfboob.htm>
- Purvis, A. and Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analyzing comparative data. – *Comput. Appl. Biosci.* 11: 247–251.
- R Development Core Team. 2004. R: a language and environment for statistical computing. -R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-00-3, URL <http://www.R-project.org>.
- Raihani, G., Székely, T., Serrano-Meneses, M. A. et al. 2006. The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae). – *Anim. Behav.* 71: 833–838.
- Rand, R. W. 1960. The biology of guano-producing seabirds 3. The distribution, abundance and feeding habits of the cormorants Phalacrocoracidae off the south west coast of the Cape Providence. – Dept of Commerce and Industries, Div. of Fisheries Investigational Rep. No, p. 42.
- Ridley, M. and Thompson, D. J. 1979. Size and mating in *Asellus aquaticus* (Curstacea: Isopoda). – *Z. Tierpsychol.* 51: 380–397.
- Sandercock, B. K. 1998. Assortative mating and sexual size dimorphism in western and semipalmated sandpipers. – *Auk* 115: 786–791.
- Sandercock, B. K. 2001. What is the relative importance of sexual selection and ecological processes in the evolution of sexual size dimorphism in monogamous shorebirds? – *Wader Study Group Bull.* 96: 64–70.
- Schreiber, E. A. and Burger, J. (eds) 2002. Biology of marine birds. – CRC Press.
- Schreiber, E. A., Schreiber, R. W. and Schenk, G. A. 1996. Red footed booby (*Sula sula*). – In: Poole, A. and Gill, F. (eds), The birds of North America. No. 241. Acad. Nat. Sci. Washington, DC: Am. Ornithol. Union.
- SEAWIFS: estimated primary productivity map, [http://marine.rutgers.edu/opp/swf/Production/results/all2\\_swf.html](http://marine.rutgers.edu/opp/swf/Production/results/all2_swf.html)
- Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. – *Condor* 68: 113–151.
- Serenty, D. L., Serenty, V. N. and Warham, J. 1971. The handbook of Australian sea-birds. – A. H. and A. W. Reed, Australia.
- Shine, R. 1979. Sexual selection and size dimorphism in the Amphibia. – *Copeia* 1979: 297–306.
- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. – *Q. Rev. Biol.* 64: 419–461.
- Sibley, C. G. and Ahlquist, J. E. 1990. Phylogeny and classification of birds. – Yale Univ. Press.
- Simons, T. R. 1985. Biology and behavior of the endangered Hawaiian dark-rumped petrel. – *Condor* 87: 229–245.
- Simons, T. R. and Hodges, C. N. 1998. Dark-rumped petrel (*Pterodroma phaeopygia*). – In: Poole, A. and Gill, F. (eds), The birds of North America. No. 13. Acad. Nat. Sci. Washington, DC: Am. Ornithol. Union.
- Smith, R. J. 1999. Statistics of sexual size dimorphism. – *J. Human Evol.* 36: 423–459.
- Sokal, R. R. and Rohlf, F. J. 1981. Biometry, 2nd ed. – Freeman.
- Székely, T., Reynolds, J. D. and Figuerola, J. 2000. Sexual size dimorphism in shorebirds, gulls, and alacids: the influence of sexual and natural selection. – *Evolution* 54: 1404–1413.
- Székely, T., Freckleton, R. P. and Reynolds, J. D. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. – *Proc. Natl Acad. Sci.* 101: 12224–12227.
- Thom, M. D., Harrington, L. A. and Macdonald, D. W. 2004. Why are American mink sexually dimorphic? A role for niche separation. – *Oikos* 105: 525–535.
- Tickell, W. L. N. 2000. Albatrosses. – Yale Univ. Press.
- Urban, E. K., Fry, C. H. and Keith, S. 1986. The birds of Africa. – Vol. 1. Academic Press.
- Webster, M. S. 1992. Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). – *Evolution* 46: 1621–1641.
- Whittow, G. C. 1993a. Black-footed albatross (*Diomedea nigripes*). – In: Poole, A. and Gill, F. (eds), The birds of North America. No. 65. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union..
- Whittow, G. C. 1993b. Laysan albatross (*Diomedea immutabilis*). – In: Poole, A. and Gill, F. (eds), The birds of North America. No. 66. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union.
- Whittow, G. C. 1997. Wedge-tailed shearwater (*Puffinus pacificus*). – In: Poole, A. and Gill, F. (eds), The birds of North America. No. 305. Acad. Natl. Sci. Washington, DC: Am. Ornithol. Union.
- Wiewandt, T. A. 1982. Evolution of nesting patterns in Iguanine lizards. – In: Burghardt, G. M. and Rand, A. S. (eds), Iguanas of the world: their behavior, ecology, and conservation. Noyes, Park Ridge, New Jersey, pp. 119–141.
- Williams, T. D. 1995. The penguins. – Oxford Univ. Press.



Appendix 1. Data used in the analyses and data sources. GR, ground display; GA, ground and aerial display; MA, mainly aerial display. Ocean primary productivity values. References: (1) Awkerman 2004 pers. comm., (2) Causey 2002, (3) Cramp and Simmons 1977, (4) Cushman-Murphy and Pennoyer 1952, (5) Diamond and Schreiber 2002, (6) Dunning 1983, (7) Evans and Knopf 1993, (8) Fleet 1974, (9) Gauger-Metz and Schreiber 2002, (10) Gould et al. 1974, (11) Harris 1970, (12) Hatch and Nettleship 1998, (13) del Hoyo et al. 1992, (14) Huntington et al. 1996, (15) Imber 1976, (16) Jeremy and Weseloh 1999, (17) Johnsgard 1993, (18) Jouventin et al. 1999, (19) Jouventin and Bried 2001, (20) Marchant and Higgins 1990, (21) Megyesi and O'Daniel 1997, (22) Metz and Schreiber 2002, (23) Monroe and Sibley 1993, (24) Nelson 1978, (25) Nelson 2002, (26) Norman and Brown 1987, (27) Provincial Museum of Alberta, Blue-footed booby, <http://www.pma.edmonton.ab.ca/vexhibit/eggs/vexeggs/wrldeggs/bfboob.htm> (28) Rand 1960, (29) Rutgers, The State Univ. of New Jersey Inst. of Marine and Coastal Sciences, <http://marine.rutgers.edu/opp>, (30) Schreiber et al. 1996, (31) Schreiber and Burger 2002, (32) Serventy et al. 1971, (33) Simons 1985, (34) Simons and Hodges 1998, (35) Tickell 2000, (36) Urban et al. 1986, (37) Whittow 1993a, (38) Whittow 1993b, (39) Whittow 1997, (40) Williams 1995.

Species	Male mass in g	Female mass in g	Clutch size	Egg size index (length in mm × breadth in mm)	Display type	Ocean productivity (g C m <sup>-2</sup> )	References
<i>Aptenodytes patagonicus</i>	16000.0	14300.0	1.00	104.10 × 73.90	GR	152	13, 20, 23, 29, 31, 40
<i>Bulweria bulwerii</i>	107.1	99.9	1.00	41.21 × 30.31	GR	180	13, 20, 21, 23, 29, 31
<i>Calonectris diomedea</i>	955.6	817.3	1.00	69.00 × 45.00	GR	180	3, 13, 23, 29, 31
<i>Daption capense</i>	442.0	407.0	1.00	61.20 × 42.60	GA	094	13, 20, 23, 29
<i>Diomedea amsterdamensis</i>	6970.0	6120.0	1.00	121.00 × 76.00	GR	141	13, 23, 29, 31, 35
<i>Diomedea bulleri</i>	3120.0	2780.0	1.00	102.16 × 66.34	GR	178	13, 20, 23, 29, 31, 32, 35
<i>Diomedea cauta</i>	4350.0	3700.0	1.00	105.00 × 67.00	GR	152	13, 20, 23, 29, 31, 35
<i>Diomedea chrysostoma</i>	3900.0	3870.0	1.00	106.00 × 68.00	GA	094	13, 20, 23, 29, 31, 35
<i>Diomedea epomophora</i>	8840.0	7560.0	1.00	126.50 × 78.50	GA	128	13, 20, 23, 29, 31, 32, 35
<i>Diomedea exulans</i>	9110.0	7270.0	1.00	133.40 × 81.00	GA	243	13, 18, 20, 23, 29, 31, 32, 35
<i>Diomedea immutabilis</i>	3310.0	2990.0	1.00	107.60 × 68.60	GR	134	13, 23, 29, 35, 38
<i>Diomedea irrorata</i>	3750.0	3040.0	1.00	105.76 × 69.06	GR	369	1, 6, 13, 23, 29, 31
<i>Diomedea melanophris</i>	3710.0	3170.0	1.00	104.00 × 66.00	GA	094	13, 20, 23, 29, 31
<i>Diomedea nigripes</i>	3400.0	2990.0	1.00	108.00 × 70.00	GR	134	13, 20, 23, 29, 37
<i>Eudyptes chrysocome</i>	2500.0	2440.0	2.00	70.50 × 53.70	GR	128	13, 20, 23, 29, 40
<i>Eudyptes chrysolophus</i>	4760.0	5210.0	2.00	70.60 × 49.10	GR	082	13, 20, 23, 29, 40
<i>Fregata andrewsi</i>	1400.0	1550.0	1.00		GA	143	13, 20, 23, 29, 31
<i>Fregata ariel</i>	754.0	858.0	1.00	64.00 × 44.00	GA	093	6, 13, 20, 23, 29, 31
<i>Fregata magnificens</i>	1281.0	1667.0	1.00	68.00 × 47.00	GA	323	5, 6, 13, 23, 29, 31
<i>Fregata minor</i>	1239.0	1630.0	1.00	67.00 × 47.40	GA	376	9, 13, 20, 22, 23, 29, 31
<i>Fregatta grallaria</i>	47.0	52.0	1.00	36.30 × 26.40	GA	317	13, 20, 23, 29, 31
<i>Fregatta tropica</i>	51.7	54.2	1.00	37.00 × 27.00	GA	106	13, 20, 23, 29
<i>Fulmarus glacialis</i>	884.0	706.0	1.00	74.00 × 51.00	GR	450	3, 6, 12, 13, 23, 29
<i>Fulmarus glacialisoides</i>	845.0	745.0	1.00	75.00 × 50.00	GR	056	13, 20, 23, 29, 31
<i>Garrodia nereis</i>	34.0	34.0	1.00	31.20 × 23.20	GR	302	13, 20, 23, 29, 31
<i>Macronectes giganteus</i>	5140.0	4220.0	1.00	104.90 × 65.70	GA	077	6, 13, 20, 23, 29
<i>Macronectes halli</i>	4902.0	3724.0	1.00	104.30 × 65.40	GA	152	13, 20, 23, 29, 31, 36
<i>Oceanites oceanicus</i>	33.6	36.2	1.00	34.90 × 24.50	MA	094	13, 20, 23, 29, 31
<i>Oceanodroma leucorhoa</i>	45.3	45.4	1.00	33.00 × 24.00	GA	266	13, 14, 20, 23, 29, 31
<i>Pachyptila desolata</i>	160.0	153.0	1.00	47.10 × 34.60	GR	094	13, 20, 23, 29
<i>Pachyptila turtur</i>	141.4	136.8	1.00	45.10 × 32.60	GR	178	13, 20, 23, 29
<i>Pagodroma nivea</i>	341.0	293.0	1.00	59.00 × 42.00	GA	094	13, 19, 20, 23, 29, 31
<i>Pelagodroma marina</i>	40.2	41.4	1.00	35.90 × 26.00	MA	411	3, 13, 23, 29
<i>Pelecanoides urinatrix</i>	110.3	101.0	1.00	40.20 × 31.60	GA	268	13, 20, 22, 23, 26, 29, 31
<i>Pelecanus erythrorhynchos</i>	6920.0	4970.0	2.00	87.10 × 57.10	GA	382	7, 13, 17, 23, 29, 31
<i>Pelecanus occidentalis</i>	3290.0	2824.0	2.60	73.00 × 45.40	GR	413	13, 17, 23, 29
<i>Pelecanus onocrotalus</i>	11450.0	7590.0	2.00	94.00 × 59.00	GR	145	3, 13, 17, 23, 29, 31
<i>Pelecanus rufescens</i>	5970.0	4920.0	1.99	82.10 × 54.60	GR	450	13, 17, 23, 29, 31, 36
<i>Phaethon rubricauda</i>	218.7	220.2	1.00	67.30 × 48.10	GA	108	8, 10, 13, 20, 23, 29
<i>Phalacrocorax auritus</i>	2453.0	2056.0	4.00	61.22 × 38.58	GA	448	13, 16, 17, 23, 29, 31
<i>Phalacrocorax capensis</i>	1171.0	1142.0	2.40	55.00 × 35.00	GR	450	13, 17, 23, 28, 29, 31
<i>Phalacrocorax capillatus</i>	3171.4	2525.0	3.00			405	13, 17, 23, 29
<i>Phalacrocorax carbo</i>	2400.0	2000.0	4.10	63.00 × 40.00	GR	243	13, 20, 23, 29, 31
<i>Phalacrocorax chalconotus</i>	2717.0	1813.6	2.50	66.00 × 42.00	GR	249	13, 20, 23, 29
<i>Phalacrocorax magellanicus</i>	1553.0	1417.0	3.00	62.00 × 38.00	GR	450	13, 17, 23, 29, 31
<i>Phalacrocorax melanoleucos</i>	800.0	700.0	4.00	47.00 × 32.00	GR	243	13, 20, 23, 29
<i>Phalacrocorax pelagicus</i>	2034.0	1702.0	3.00	58.00 × 37.30	GR	382	13, 17, 23, 29, 31
<i>Phalacrocorax punctatus</i>	1210.0	1160.0	2.70	59.40 × 36.80	GR	411	13, 20, 23, 29, 31
<i>Phalacrocorax purpurascens</i>	3320.0	2700.0	2.74	64.00 × 40.00	GR	077	13, 20, 29
<i>Phalacrocorax sulcirostris</i>	1100.0	900.0	5.00	47.00 × 33.00	GR	243	13, 17, 20, 23, 29, 31
<i>Phalacrocorax urile</i>	2428.1	1874.4	3.08	61.40 × 37.40	GR	382	2, 13, 17, 23, 29, 31
<i>Phalacrocorax varius</i>	1800.0	1400.0	3.32	59.00 × 38.00	GR	428	13, 17, 20, 23, 29
<i>Phoebastria fusca</i>	2800.0	2700.0	1.00	103.10 × 65.10	GA	152	13, 20, 23, 29, 31
<i>Procellaria aequinoctialis</i>	1390.0	1280.0	1.00	82.90 × 53.70	GA	094	13, 20, 23, 29
<i>Procellaria parkinsoni</i>	723.0	682.0	1.00	69.30 × 50.50	GR	360	13, 20, 23, 29, 31

## Appendix 1 (continued)

Species	Male mass in g	Female mass in g	Clutch size	Egg size index (length in mm × breadth in mm)	Display type	Ocean productivity (g C m <sup>-2</sup> )	References
<i>Procellaria westlandica</i>	1232.5	1176.0	1.00	81.10 × 55.60	GR	450	13, 20, 23, 29
<i>Pterodroma brevirostris</i>	246.0	230.3	1.00	57.40 × 44.90		243	13, 20, 23, 29
<i>Pterodroma inexpectata</i>	302.0	335.1	1.00	60.53 × 43.90	MA	253	13, 20, 23, 29, 31
<i>Pterodroma macroptera</i>	668.0	667.0	1.00	67.50 × 48.30	MA	057	4, 6, 13, 15, 20, 23, 29, 31
<i>Pterodroma nigripennis</i>	169.6	165.9	1.00	51.00 × 37.00	MA	302	13, 20, 23, 29
<i>Pterodroma phaeopygia</i>	430.0	429.0	1.00	65.00 × 45.00	GA	376	11, 13, 23, 29, 31, 33, 34
<i>Puffinus bulleri</i>	345.0	306.5	1.00	65.44 × 42.96	GR	411	13, 20, 23, 29, 31
<i>Puffinus pacificus</i>	457.0	474.6	1.00	61.40 × 41.10	GR	317	13, 20, 23, 29, 31, 39
<i>Pygoscelis antarctica</i>	4435.0	3876.0	2.00	67.20 × 52.00	GR	396	13, 20, 23, 29, 40
<i>Pygoscelis papua</i>	5860.0	5070.0	2.00	68.10 × 57.70	GR	094	13, 20, 23, 29, 31
<i>Papasula abbotti</i>	1472.6	1491.5	1.00	82.00 × 53.00	GR	094	13, 20, 23, 29, 31
<i>Morus bassanus</i>	2932.0	3067.0	1.00	79.00 × 50.00	GA	450	13, 23, 24, 25, 29, 31
<i>Morus capensis</i>	2665.0	2608.0	1.00	76.13 × 48.22	GR	450	13, 20, 23, 24, 29, 31, 36
<i>Sula dactylatra</i>	2000.0	2533.3	2.00	66.30 × 46.50	GA	210	13, 20, 23, 29, 31
<i>Sula leucogaster</i>	1188.6	1343.6	2.00	61.00 × 40.00	GA	248	13, 20, 23, 29, 31
<i>Sula nebulxii</i>	1283.0	1801.0	2.00	57.00 × 41.00	MA	376	6, 13, 23, 24, 27, 29, 31
<i>Sula sula</i>	928.0	1068.0	1.00	60.80 × 41.00	GA	245	13, 20, 23, 29, 30, 31
<i>Thalassoica antarctica</i>	663.0	627.0	1.00	70.00 × 48.80	GA	056	6, 13, 20, 23, 29, 36

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.