

Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere

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Fairbairn, J. and Shine, R. 1993. Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. – *Oikos* 68: 139–145.

A review of published data on 99 populations (60 species) of seabirds shows that the degree of sexual size dimorphism varies considerably among species, with males larger than females in some species but smaller in others. Males tend to be larger, relative to females, in populations (1) that have large average body mass, and (2) that feed in areas of the ocean (especially, high latitudes) where primary productivity is high. These correlations are not due to phylogenetic conservatism, because the relationships hold even when the data are analysed cladistically. These patterns are similar in some respects to those seen in other avian lineages, but their adaptive significance remains unclear.

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Males grow larger than females in most species of birds, but “reversed size dimorphism” (= RSD, where females are the larger sex) has evolved independently in a number of avian lineages, notably in the raptors, owls, shorebirds and seabirds. Although many evolutionary hypotheses have been proposed to explain the occurrence and degree of RSD in birds, scientific interest in this question has focussed overwhelmingly on raptors (e.g., Wheeler and Greenwood 1983, Mueller and Meyer 1985). Much less attention has been paid to owls (but see Earhart and Johnson 1970, Snyder and Wiley 1976, Andersson and Norberg 1981) or shorebirds, and even less attention to seabirds (but see Jehl and Murray 1986). Many of the hypotheses derived from studies on other types of birds fail to predict RSD in seabirds (Andersson and Norberg 1981, Jehl and Murray 1986, Schreiber and Schreiber 1988). Nonetheless, the sub-order Ciconii offers excellent opportunities for the comparative analysis of sexual size dimorphism. Although many potentially confounding factors are held constant (e.g., all species are monogamous, with both parents contributing to the rearing of the young; the sexes are generally similar in external appearance, except in frigate birds), seabirds include a wide diversity of species

in terms of geographic distributions, foraging strategies, social organisation and sexual dimorphism. In the present paper, we review published information to document morphological and ecological correlates of sexual size dimorphism within the Ciconii.

Materials and methods

We gathered data on all marine species from the recent handbook by Marchant and Higgins (1990). For each population for which separate data were available, we took information on (1) mean body masses for adult males and females, (2) mean clutch sizes, (3) mean nest densities (nests/m²), and (4) we recorded the location of the breeding site at which those measurements had been taken. For each of these breeding sites we then determined minimum levels for rates of primary production of the surrounding ocean (rate of carbon fixation in g/m², to the nearest 50 g) from a global map of this variable (Löfgren 1984). Mean adult body mass for each species was calculated as the average of mean masses of

Accepted 11 December 1992

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Table 1. Sexual size dimorphism in seabirds of the Southern Hemisphere. “SSD” index of sexual dimorphism in mean adult body mass (= [larger sex divided by smaller sex] – 1.0, arbitrarily positive if female larger, negative if male larger); “minimum carbon fixation” = lower end of range of primary estimate for ocean surrounding breeding site (see text); “nests/m²” = mean nest density.

Family	species	male mass (g)	female mass (g)	mean adult mass (g)	SSD	minimum carbon fixation (g/m ²)	mean clutch	nests/m ²
Phaethontidae Sulidae	<i>Phaethon lepturus</i>	262.4	305	283.7	0.16	0	1	–
	<i>Morus capensis</i>	2665	2608	2636.5	–0.02	100	1	2.30
	<i>Sula abbotti</i>	1472.6	1491.5	1482.1	0.01	–	1	–
	<i>Sula abbotti</i>	1410.4	1467.6	1439	0.04	0	–	–
	<i>Sula dactylatra</i>	2000	2533	2266.5	0.27	50	1.6	–
	<i>Sula dactylatra</i>	1677	1852	1764.5	0.10	50	–	–
	<i>Sula dactylatra</i>	1503	1616	1559.5	0.08	0	–	–
	<i>Sula leucogaster</i>	1188.6	1343.6	1266.1	0.13	50	2.01	–
	<i>Sula leucogaster</i>	1086.6	1350	1218.3	0.24	50	–	–
	<i>Sula leucogaster</i>	962	1260	1111	0.31	0	–	–
	<i>Sula leucogaster</i>	1066.2	1198.5	1132.3	0.12	–	–	–
	<i>Sula leucogaster</i>	1056	1175	1115.5	0.11	50	–	0.08
	<i>Sula sula</i>	938	1068	1003	0.14	–	–	–
Phalacrocoracidae	<i>Phalacrocorax punctatus</i>	1210	1160	1185	–0.04	100	2.7	1.05
	<i>Phalacrocorax chalconotus</i>	2717	1813.6	2265.3	–0.50	200	2.5	1.05
	<i>Phalacrocorax chalconotus</i>	2500	2500	2500	0.00	200	–	–
	<i>Phalacrocorax georgianus</i>	2883.2	2472.7	2677.9	–0.17	200	3	0.70
	<i>Phalacrocorax bransfieldensis</i>	3022	2576	2799	–0.17	100	2.5	0.50
	<i>Phalacrocorax melanogensis</i>	2450	2040	2245	–0.20	200	2.9	9.00
	<i>Phalacrocorax purpurascens</i>	2860	2430	2645	–0.18	–	–	–
	<i>Phalacrocorax purpurascens</i>	3320	2700	3010	–.23	200	2.74	0.54
	<i>Phalacrocorax verrucosus</i>	2000	1600	1800	–0.25	200	3	–
	Fregatidae	<i>Fregata minor</i>	1210	1427	1318.5	0.18	50	1
<i>Fregata minor</i>		1239	1630	1434.5	0.32	0	–	–
<i>Fregata andrewsi</i>		1400	1550	1475	0.11	50	1	–
<i>Fregata ariel</i>		–	–	–	–	50	1	2.43
Spheniscidae	<i>Aptedonytes patagonicus</i>	12800	11500	12150	–0.11	200	1	2.20
	<i>Aptedonytes patagonicus</i>	16000	14100	15050	–0.14	200	1	1.30
	<i>Aptedonytes forsteri</i>	38200	29500	33850	–0.30	200	1	8.70
	<i>Pygoscelis papua</i>	6400	5500	5950	–0.16	–	2	1.05
	<i>Pygoscelis adeliae</i>	6000	5400	5700	–0.11	100	2	2.13
	<i>Pygoscelis antarctica</i>	4130	3920	4025	–0.05	100	2	2.43
	<i>Pygoscelis antarctica</i>	4435	3876	4155.5	–0.14	100	2	–
	<i>Eudyptula minor</i>	1063	945	1004	–0.13	200	2	4.10
	<i>Eudyptula minor</i>	1172	1048	1110	–0.12	50	2	–
	<i>Megadyptes antipodes</i>	8500	7500	8000	–0.13	200	2	–
	<i>Eudyptes chrysocome</i>	2500	2440	2470	–0.03	200	2	2.20
	<i>Eudyptes chrysocome</i>	2760	2400	2580	–0.15	200	2	–
	<i>Eudyptes chrysocome</i>	3420	2230	2825	–0.53	200	2	–
	<i>Eudyptes chrysocome</i>	2700	2500	2600	–0.08	200	2	–
	<i>Eudyptes pachyrhynchus</i>	4936	4820	4878	–0.02	–	2	0.23
<i>Eudyptes sclateri</i>	6382	5434	5908	–0.17	200	2	0.71	
<i>Eudyptes shlegeli</i>	4500	4000	4250	–0.13	200	2	2.43	
Procellariidae	<i>Oceanites oceanicus</i>	39.2	40	39.6	0.02	–	–	–
	<i>Oceanites oceanicus</i>	36.5	40	38.2	0.10	50	1	0.12
	<i>Oceanites oceanicus</i>	34	34	34	0.00	50	–	–
	<i>Oceanites nereis</i>	32.4	32.6	32.5	0.01	200	1	–
	<i>Fregatta tropica</i>	56	56.5	56.2	0.01	–	–	–
	<i>Fregatta tropica</i>	51.7	54.2	53	0.05	200	1	–
	<i>Fregatta grallaria</i>	47	52	49.5	0.11	50	1	–
	<i>Pelagodroma marina</i>	40.2	41.4	40.8	0.03	200	1	11.71
	<i>Macronectes halli</i>	4711.1	3370.8	4041	–0.40	200	1	0.11
	<i>Macronectes halli</i>	4790	3580	4185	–0.34	200	1	–
	<i>Macronectes halli</i>	4930	3950	4440	–0.25	200	1	0.11
	<i>Macronectes giganteus</i>	4902	3724	4313	–0.32	200	1	–
	<i>Macronectes giganteus</i>	5140	4220	4680	–0.22	200	1	–
	<i>Macronectes giganteus</i>	4940	3850	4395	–0.28	–	1	–
	<i>Pterodroma brevirostris</i>	246	230	238	–0.07	50	1	3.00
	<i>Pterodroma brevirostris</i>	302	335	318.5	0.11	–	–	–
	<i>Pterodroma solandri</i>	517	423.5	470.2	–0.22	50	1	–
	<i>Pterodroma cooki</i>	164	192.7	178.4	0.18	50	1	–
	<i>Pterodroma cervicalis</i>	448.7	436.2	442.5	–0.03	1	–	–
	<i>Pterodroma nigripennis</i>	169.6	165.9	167.8	–0.02	100	1	1.56

Table 1. Continued

Family	species	male mass (g)	female mass (g)	mean adult mass (g)	SSD	minimum carbon fixation (g/m ²)	mean clutch	nests/m ²
	<i>Bulweria bullwerii</i>	107.1	99.9	103.5	-0.07	50	1	-
	<i>Procellaria parkinsoni</i>	723	682	702.5	-0.06	50	1	-
	<i>Procellaria cinerea</i>	1073	989	1031	-0.09	200	1	1.00
	<i>Puffinus pacificus</i>	457	474.6	465.8	0.04	0	1	0.33
	<i>Puffinus bulleri</i>	345	306.5	325.8	-0.13	100	1	0.08
	<i>Puffinus tenuirostris</i>	560	528	544	-0.06	100	1	1.00
	<i>Puffinus gavia</i>	221.2	236.9	229	0.07	50	1	0.06
	<i>Fulmarus glacialis</i>	845	745	795	-0.13	-	1	-
	<i>Daption capense</i>	442	407	424.5	-0.09	-	1	-
	<i>Daption capense</i>	452	419	435.5	-0.08	200	1	-
	<i>Pagodroma nivea</i>	367.2	341	354.1	-0.08	100	1	0.54
	<i>Pagodroma nivea</i>	439	358.2	398.6	-0.23	-	-	-
	<i>Pagodroma nivea</i>	341	293	317	-0.16	100	-	-
	<i>Pagodroma nivea</i>	317	291	304	-0.09	-	-	-
	<i>Pagodroma nivea</i>	332	244	288	-0.36	-	-	-
	<i>Pagodroma nivea</i>	276	263	269.5	-0.05	-	-	-
	<i>Pagodroma nivea</i>	268.5	246.2	257.4	-0.09	-	-	-
	<i>Pagodroma nivea</i>	292.7	246.2	269.5	-0.19	-	-	-
	<i>Pagodroma nivea</i>	258	229.8	243.9	-0.12	-	-	-
	<i>Holobaena caerulea</i>	134	124.4	129.2	-0.08	100	1	2.00
	<i>Pachyptila desolata</i>	160	153	156.5	-0.05	200	1	-
	<i>Pachyptila turtur</i>	141.4	136.8	139.1	-0.03	200	1	1.03
	<i>Pachyptila turtur</i>	115.4	117.7	116.6	0.02	100	1	-
	<i>Phoebetria fusca</i>	2600	2400	2500	-0.08	-	1	-
	<i>Phoebetria fusca</i>	2730	2440	2585	-0.12	200	1	0.17
	<i>Diomedea melanophrys</i>	3710	3170	3440	-0.17	200	1	0.51
	<i>Diomedea bulleri</i>	3120	2780	2950	-0.12	200	1	2.80
	<i>Diomedea cauta</i>	4350	3700	4025	-0.18	-	1	2.43
	<i>Diomedea cauta</i>	4430	3450	3940	-0.28	200	1	-
	<i>Diomedea cauta</i>	4000	3590	3795	-0.11	200	1	-
	<i>Diomedea chrysostoma</i>	3380	2980	3180	-0.13	200	1	-
	<i>Diomedea chrysostoma</i>	3680	3610	3645	-0.02	200	1	0.68
	<i>Diomedea epomophora</i>	8900	7600	8250	-0.17	200	1	-
	<i>Diomedea epomophora</i>	10300	7700	9000	-0.34	200	1	0.00
	<i>Diomedea exulans</i>	9768	7686	8727	-0.27	200	1	0.04
	<i>Diomedea exulans</i>	7350	5670	6510	-0.30	200	1	-

males and females. Our justification for choosing these variables for analysis was as follows:

- (1) absolute body size has been shown to influence the degree of sexual size dimorphism in some other types of animals (e.g., Clutton-Brock et al. 1977, Berry and Shine 1980);
- (2) selection for increased clutch size might influence female body sizes (e.g., Darwin 1871);
- (3) high-density nesting might impose selection for an enhanced capacity for nest defence in one or both sexes, and hence favour larger body sizes (Jehl and Murray 1986);
- (4) low food availability might constrain the range of ecologically achievable body sizes of males and females (and thus, the degree of dimorphism), or favour sex-specific partitioning of foraging niches (e.g., Selander 1966, 1972). Sex differences in feeding territories may occur in seabirds (Nelson 1978, Weimerskirch et al. 1985), and body-size differences between the sexes may affect dive depth (and

hence, dietary composition) in plunge divers such as sulids (Nelson 1980).

Although simple ratios of male to female size are often used as indices of sexual size dimorphism, their use may introduce significant statistical artifacts (Atchley et al. 1976). Instead, we calculated the index of dimorphism recommended by Gibbons and Lovich (1990, and unpubl.). Their method involves (1) calculating the ratio of the body size of the larger sex to that of the smaller sex, (2) subtracting a value of 1.0 from this ratio, and (3) arbitrarily defining the resulting number as positive if females are the larger sex, and as negative if males are larger. This procedure yields an index of sexual size dimorphism which is symmetrical around zero (= no dimorphism), and hence is amenable to statistical analysis (Gibbons and Lovich 1990, and unpubl.).

We analysed these data in two different ways. First, we looked for correlations between the degree of sexual size dimorphism and the other variables by treating each population as an independent unit. This type of

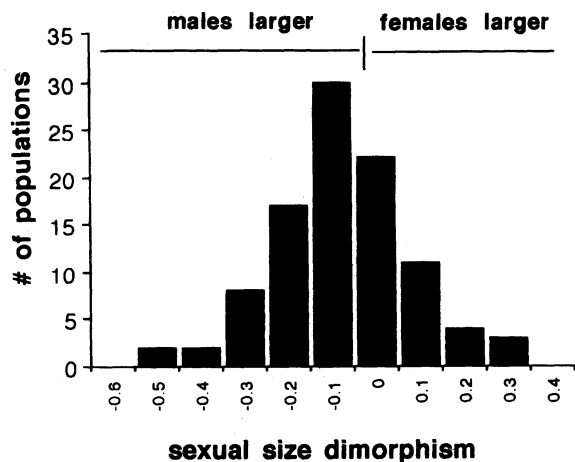


Fig. 1. The degree of sexual size dimorphism in Southern Hemisphere seabirds (infraorder Ciconiides), based on data from 99 populations (60 species). Negative values show populations with males exceeding females in mean adult body mass; positive values show populations where females grow larger than males.

analysis gives considerable statistical power (due to the large number of degrees of freedom) and is relatively easy to interpret. However, it may be misleading because it ignores the fact that two characteristics may be correlated in occurrence not because of any functional relationship (i.e., X imposes a selective pressure for Y), but instead because of phylogenetic conservatism (i.e., X and Y co-occur because they are both inherited from some common ancestor with this combination of traits) (Harvey and Pagel 1991). In order to determine whether any of the correlations we detected were due to this kind of phylogenetic conservatism, we repeated our analyses using Pagel and Harvey's (1989) program to quantify and compare independent evolutionary contrasts in the relevant variables. This program superimposes the data for each species onto a phylogeny of the entire group, and calculates a series of independent comparisons based on the branching sequences of the phylogeny. We used the phylogenetic hypotheses of Sibley and Ahlquist (1990) as the basis for our analysis, in conjunction with more detailed (especially, intrageneric) phylogenetic reconstructions for specific groups (Zusi 1975, Imber 1985, Seigel-Causey 1988). We did not attempt to reconstruct intraspecific relationships, so all intraspecific phylogenies were unresolved in our analysis.

Results

We obtained information on 99 populations of Southern Hemisphere seabirds, comprising 60 species. The direction of sexual size dimorphism showed considerable interspecific variation, but phylogenetic conservatism

was obvious in most groups at both the specific and generic levels (Table 1). Males grow much larger than females in some taxa (e.g., AnHINGIDAE, PHALACROCORACIDAE, SPHENISCIDAE) whereas females are larger than their mates in others (notably the tropicbirds, Phaethontidae). Within the Sulidae, males are larger than females in most or all species of gannets, whereas females are the larger sex in boobies. Most tubenoses (Procellariidae) have males larger than females, but the reverse occurs in some species. Overall, male-biased dimorphism was more common than female-biased dimorphism (Fig. 1).

Our analysis using populations as independent units showed that the degree of sexual size dimorphism in seabirds was not significantly associated with either clutch size ($r = 0.21$, $n = 76$, $P = 0.07$) or the density of nests in breeding areas ($r = 0.06$, $n = 37$, $P = 0.70$), but that the degree of dimorphism was significantly correlated with mean adult body mass (data on body mass

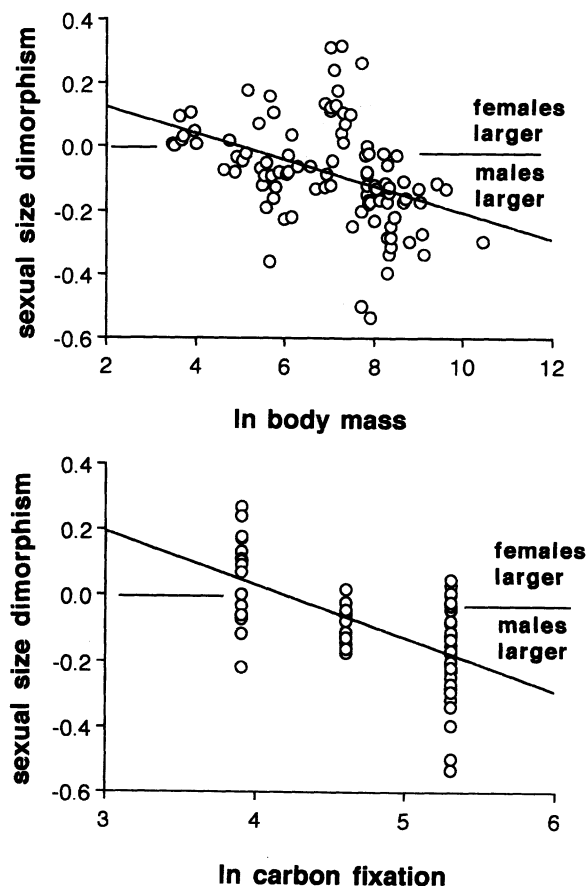


Fig. 2. Populations of breeding seabirds show more male-biased dimorphism in body size (i.e., males are relatively larger) in species of larger average body mass (top) and in areas where oceanic productivity is higher (bottom). For body mass: $SSD = -0.04 \times \ln \text{mean body mass} + 0.21$; $r = 0.40$, $n = 98$, $P < 0.001$; for carbon fixation: $SSD = -0.16 \times \ln \text{carbon fixation rate} + 0.68$; $r = 0.62$, $n = 72$, $P < 0.001$.

were log-transformed to normalise variances: $r = 0.40$, $n = 98$, $P < 0.001$). Males tended to be larger, relative to females, in larger species (Fig. 2). Dimorphism was also significantly more male-biased in populations breeding on islands surrounded by oceans with high primary productivity (using log-transformed values for carbon fixation rates: $r = 0.62$, $n = 72$, $P < 0.001$; Fig. 2). Do these two correlates of sexual size dimorphism represent independent effects, or are they intercorrelated themselves such that one of these significant associations is simply a consequence of the other? Our data confirm that larger species tend to live in areas of higher productivity ($r = 0.45$, $n = 71$, $P < 0.001$), but further analysis shows that this intercorrelation cannot explain our earlier results. We carried out a stepwise multiple regression with sexual size dimorphism as the dependent variable, and mean adult body mass and primary productivity as the independent variables. Both of these independent variables contributed significantly to the observed variance in sexual size dimorphism, even after the effect of the other variable was removed from the analysis (overall $F_{2,70} = 27.01$; F to remove mean adult body mass = 6.94; F to remove carbon fixation rate = 24.36; $P < 0.05$ in both cases).

The phylogenetically-based analysis (Pagel and Harvey 1989) confirmed these results, suggesting that the patterns evident from straightforward comparisons at the populational level were due to consistent functional relationships among these variables rather than to phylogenetic conservatism. No significant correlation was evident between the magnitudes of evolutionary shifts in sexual size dimorphism and concurrent evolutionary changes in the density of nests in breeding areas ($r = 0.14$, $n = 13$, $P = 0.65$) or in clutch sizes ($r = 0.36$, $n = 13$, $P = 0.23$). However, phylogenetic shifts in sexual size dimorphism were significantly associated with concurrent shifts in mean adult body mass ($r = 0.66$, $n = 13$, $P < 0.02$) and with shifts in the primary productivity of waters surrounding the breeding site ($r = 0.56$, $n = 13$, $P < 0.05$). Because phylogenetic changes in mean body sizes and in the primary productivity of breeding areas are themselves highly correlated ($r = 0.83$, $n = 13$, $P < 0.001$), the relationships between these two variables and sexual size dimorphism may not represent independent effects. Although we were able to falsify this interpretation in the analysis using populations as independent units (above), we could not do so in terms of phylogenetic shifts. Stepwise multiple regression, with evolutionary contrasts in sexual size dimorphism as the dependent variable, showed that shifts in primary productivity did not explain significant additional variation in dimorphism once changes in adult body mass had been incorporated into the regression ($F_{1,12} = 8.51$; F to remove change in mass = 8.51; F to remove change in productivity = 0.004). Hence, the trend for a higher degree of male-biased size dimorphism in areas of higher primary productivity may be an incidental consequence of the trend for larger body size in these areas.

However, it is important to note that the power of this test is relatively low, and our ability to disentangle these effects – even if they are separate – is thus very limited.

Discussion

Our analyses of published data on Southern Hemisphere seabirds show that the degree to which the mean body size of males exceeds that of conspecific females varies with absolute body size. Larger species have relatively larger males. Although there is a clear trend for some lineages to have both large size and male-biased dimorphism, whereas other lineages have small size and female-biased dimorphism, the correlation between absolute size and the degree of dimorphism remains significant even after this effect has been eliminated from the analysis. Thus, the allometry of sexual size dimorphism in these birds is not due to phylogenetic conservatism. Studies on a wide variety of other types of animals have provided evidence for a similar allometry of the degree of sexual size dimorphism. For example, a trend for females to be the larger sex in small species, but males the larger sex in larger species, is seen in frogs (Shine 1979), turtles (Berry and Shine 1980, Iverson 1990), and several groups of mammals (Ralls 1976, Clutton-Brock et al. 1977, Jarman 1983). Allometry of the degree of dimorphism is evident in some other types of birds with RSD, including hummingbirds (Payne 1984), owls (Mueller 1986) and diurnal raptors (Mueller 1990). Hence, some very general explanation may be most appropriate (although, see Reiss 1989 for an alternative view). We thus will not attempt to frame any hypotheses for this trend with respect to the specific ecological or morphological attributes of seabirds.

The other significant correlate of sexual size dimorphism in seabirds revealed by our analyses, both in terms of inter-population patterns and in concurrent phylogenetic shifts, was the primary productivity (carbon fixation rate) in the waters surrounding the breeding sites of the birds. Ocean productivity tends to be lowest near the equator (Löfgren 1984), and the rich Antarctic convergence supports large numbers of seabirds, primarily penguins, albatross, petrels and gannets (Nelson 1980). Away from these nutrient-rich areas (i.e., at lower latitudes), seabirds tend to be smaller in terms of mean adult body mass, to have females relatively larger than males, and to forage in areas of lower primary productivity. A similar correlation between latitude and the degree of RSD was suggested for owls by Lundberg (1986), but has been disputed by Mueller (1990).

The extensive literature on sexual size dimorphism in birds contains a plethora of hypotheses on the advantages of particular directions and degrees of dimorphism, and little consensus has been achieved (see above references). Of the many hypotheses derived

from work on other kinds of birds, the following three seem best able to predict or explain our data on seabirds:

- (1) larger size in incubating females may offer a buffer against starvation if foraging is unsuccessful in the nutrient-poor waters of the tropics (cf. Downhower 1976, Jönsson and Alerstam 1990);
- (2) the need for tropical seabirds to forage more widely (because of low productivity of the tropical oceans) and their tendency to feed on more elusive prey (such as flying-fishes) may favour small body sizes in males, because of the enhanced efficiency (lowered flight costs) of smaller body mass. Hence, RSD in these groups fits the “foraging profitability” pattern seen in raptors (e.g., Wheeler and Greenwood 1983, Mueller and Meyer 1985) and shorebirds (Jönsson and Alerstam 1990);
- (3) the relatively low nesting densities of tropical and subtropical seabirds may reduce the importance of nest-site establishment and defence by males, and hence the intensity of intrasexual selection for large body size in this sex. Aerial displays (as in tropicbirds) or the use of visual signals (as in frigatebirds) may take the place of direct combat, and hence reduce the advantage of large body size in males (e.g., Jehl and Murray 1986, Mueller 1990).

Unfortunately, broad correlational analyses like the present one may help to suggest hypotheses for further study, but cannot establish causal connections. We need more detailed information on the ecological consequences of different body sizes, and different degrees of dimorphism, before speculating further. Correlational analyses have many shortcomings, chief of which is the possibility that several variables may be so tightly intercorrelated that it is impossible to tease them apart. For example, oceanic primary productivity also correlates with many other biologically important characteristics (e.g., environmental temperatures, length of the breeding season, availability of breeding sites, migration distances, nest site fidelity, climatic predictability, predator densities). Hence, the apparent influence of oceanic productivity on sexual size dimorphism in seabirds may be mediated through some other variable not considered in the current study. The literature on raptors and shorebirds contains many examples of approaches that could usefully be applied to seabirds. The potential of such studies is very great, because any general understanding of the phenomenon of “reversed sexual dimorphism” in birds must incorporate seabirds as well as the more intensively studied avian taxa.

Acknowledgements – We thank the Australian Research Council for financial support, and W. Boles and G. Phipps for comments on the manuscript.

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