Sexual size dimorphism in seabirds: a reply to Croxall

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Croxall (1995) has attacked our analysis of sexual size dimorphism in southern-Hemisphere seabirds (Fairbairn and Shine 1993) on several grounds, and suggested that our conclusions are in error because of deficiencies in the ways that we compiled and analysed our data sets. We believe that he is wrong, and we explain our reasons in this rebuttal.

Croxall's major arguments are as follows: (1) our estimates of mean body sizes for males and females of several taxa are unreliable, because they contain numerous errors, omit important species, are based on samples that vary considerably in size and reliability, and do not take into account short-term fluctuations in body mass in breeding seabirds. (2) the direction and degree of sexual size dimorphism (SSD) in seabirds show strong phylogenetic conservatism, so that the associations we documented between SSD and two other variables (absolute body size, and oceanic productivity) may be artifacts of phylogenetic conservatism in these variables also.

First, we consider Croxall's criticisms of our data set. He identified only one mathematical error (a transposition of two digits for mean mass of males in one population of rockhopper penguins) among our data on 99 populations (66 species) of seabirds. However, Croxall also identified numerous other problems: his Appendix lists 17 populations that we omitted despite the availability of published data, three data sets that combined information gathered in different ways (one sample of *Diomedea exulans* was gathered during the breeding season whereas another was not; one sample of *Fregetta tropica* was based on measurements of live animals whereas another was not; the data for *Oceanites nereis* combined data from different localities) and four data sets that were based on "inadequate" information (small sample sizes for *Pterodroma solandi*, *P. cooki*, and *Puffinus gavia*; reliance on beachcast specimens for *Pterodroma brevirostris*). He also criticised the use of a temporally unstable measure such as body mass as an index of size di-

morphism. Below, we consider each of these issues in turn.

First, we consider the omissions. As our paper indicated, we relied on a single encyclopedic review (Marchant and Higgins 1990). Two of the omissions cited by Croxall concern taxa (*Diomedea m. melanophrys* and *D. chrysostoma*) that were not listed in this review, and hence were not incorporated in our study for this reason. Another supposed omission (of a very large data set for *Eudyptula minor*) is an error on Croxall's part: the sample is incorporated in our Table and in our analysis. However, Croxall also identified 15 additional taxa that were listed in Marchant and Higgins (1990), but which we did not include. Ironically, in view of Croxall's concerns about small sample sizes, we had omitted 9 of these samples because they were based on small numbers (≤ 10 specimens of one sex). The other six "missing" populations were omitted inadvertently, or because we had the same kinds of reservations as Croxall about using samples based only on skins rather than live birds. We have repeated our analyses with the full data set (i.e., incorporating all taxa listed in Marchant and Higgin's review, including the 15 identified by Croxall and three others also omitted from the original analysis). Our conclusions are unchanged. In analyses that treat each population as an independent unit, SSD correlates significantly both with mean absolute adult body mass ($n = 118$, $r = -0.44$, $P < 0.0001$) and with oceanic productivity ($n = 100$, $r = -0.55$, $P < 0.0001$). The same patterns remain with a phylogenetically based analysis, where the magnitudes of phylogenetic changes in one variable are compared to concurrent changes in another variable (SSD vs size $n = 54$, $r = -0.29$, $P < 0.035$; SSD vs productivity $n = 57$, $r = -0.36$, $P < 0.007$). Thus, incorporating these additional taxa has no influence on our conclusions.

Croxall also raises a more general issue of omission of taxa, by suggesting that we should have included additional species from other parts of the world. It is un-

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doubtedly true that patterns of association among variables may differ among lineages, and within lineages among different geographical areas (e.g., Harvey and Pagel 1991). However, the existence of such spatial variation does not negate the value of looking at a subset of taxa from a single region, thereby controlling for other sources of ecological variation. It will always be true that any comparative analysis is based on a subset of species (those that have not gone extinct over the preceding few million years, and those for which data are available), and the same is self-evidently true when attention is focussed on the population level rather than the species level (as for many of our comparisons). We thus defend the notion of an analysis based on a subset of taxa: it is clearly impossible to include all living organisms in any analysis, and it makes perfect sense to restrict comparisons geographically. Broader analyses would be valuable, but they do not invalidate our own study.

The next point we consider concerns the reliability of the data we used. Croxall is undoubtedly correct in pointing out that some of our size estimates for populations are based on very few specimens, and in some cases the data have been gathered in different ways. It is also true that body mass is only one of several potential descriptors of overall size, and that seabirds often change substantially in mass over the course of the breeding season. However, he is wrong in his conclusion that these undeniable features of our data set cast serious doubts on the conclusions we draw from our analysis.

The reason is straightforward. Errors introduced into comparative analyses by unreliable data will not spontaneously generate significant associations among the variables under study (e.g., Shine 1987). Instead, so long as the errors are random with respect to the putative associations among variables, imprecision in estimates of relevant variables will reduce rather than inflate the strength of any patterns that are detected. Thus, the only conclusions that would be weakened by a demonstration of random errors in the data, would be conclusions that relied upon acceptance of the null hypothesis (i.e., that there is no significant pattern of association among variables). If, instead, the analysis reveals strong and significant associations (as was the case with our work), despite wide confidence intervals in the data used to generate the analyses, then the underlying patterns of association are probably even stronger than were suggested by the original analysis (Shine 1987). Hence, the sources of imprecision emphasised by Croxall strengthen rather than weaken our conclusions. His criticism would invalidate our analyses only if there was a consistent error that was non-random with respect to the hypotheses under study (e.g., SSD was spuriously reported as more highly male-biased in species of larger mean body size). If the error simply results from insufficiently precise data, it will not introduce spurious associations among variables.

Croxall's second major criticism was related to the fact that seabirds display considerable phylogenetic conserva-

tism in traits such as SSD, absolute body size, and geographic distribution (and hence, oceanic productivity). As our Table shows, he is undoubtedly correct in this statement. Croxall then infers that this conservatism invalidates our conclusions, because "the pattern of sexual dimorphism in seabirds reflects particular species or group-specific traits, rather than a general underlying relationship with body size or oceanic productivity". This is a valid criticism of any "tips" analysis, which assumes that species are independent data points (Harvey and Pagel 1991). However, our phylogenetically based analysis was designed to deal with exactly this problem. It calculates phylogenetic changes in one trait (such as mean adult body size) and compares the magnitude of such changes to concurrent shifts in another trait (such as SSD) within the same clade. Thus, phylogenetic conservatism cannot produce a significant association between variables in this type of analysis. Croxall clearly misunderstands the nature of our phylogenetically based analysis. He contends that "the overall relationship [between SSD and body size] simply reflects that the lightest seabirds (storm petrels) show consistently female-biased dimorphism and that the heaviest ones (albatrosses, giant petrels) show the greatest male-biased dimorphism". In fact, our analyses refute this interpretation: we show that phylogenetic changes in mean body size are significantly correlated with concurrent phylogenetic changes in SSD. This result indicates that there is a consistent (and hence, probably a functional) relationship between the evolution of larger size and the evolution of SSD in a whole series of phylogenetically controlled comparisons: of populations within species, species within genera, genera within families, and so forth. Because the analysis is phylogenetically based, phylogenetic conservatism in the traits under study cannot affect the results obtained.

In summary, Croxall's criticisms are in error. Firstly, incorporating the additional taxa listed in his Appendix 1 does not change any of our significant results. Secondly, imprecision in our body-size estimates will not generate spurious correlations among variables. And thirdly, because our methods of analysis were phylogenetically based, their results cannot be attributed to phylogenetic conservatism. Although we thus disagree violently with Croxall's criticisms, we agree with many of his comments. Thus, for example, his suggestions that the correlation between SSD and oceanic productivity may not reflect a causal relationship, and that many additional factors are likely to influence SSD in seabirds, mirror conclusions from our own analysis. We also concur with his call for more comprehensive field studies of seabirds, and for comparative analyses of patterns of SSD in seabird taxa not included in our original analyses. Our paper attempted to identify patterns of variation in SSD among these organisms, emphasised the difficulty of drawing any clear conclusions from the available data, and called for additional research on this topic. We are gratified that this call has been answered so promptly, even if we disagree with much that has been said.

References

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