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Opinion is intended to facilitate communication between reader and author and reader and reader. Comments, viewpoints or suggestions arising from published papers are welcome. Discussion and debate about important issues in ecology, e.g. theory or terminology, may also be included. Contributions should be as precise as possible and references should be kept to a minimum. A summary is not required.

Sexual size dimorphism in seabirds

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In their paper on patterns of sexual size dimorphism in seabirds of the Southern Hemisphere, Fairbairn and Shine (1993) concluded that: a) sexual dimorphism is related to body size with larger species showing greater male-based dimorphism; and b) female-biased sexual dimorphism is greater in areas of poorer productivity (i.e. in the tropics).

In this note I wish to suggest that neither of these conclusions may be valid, because: a) different groups of seabirds tend to show characteristic degrees of sexual dimorphism and size is only one factor influencing this; and b) restricting consideration to species covered in Marchant and Higgins (1990) [The Handbook of Australian, New Zealand and Antarctic Birds – hereafter abbreviated to HANZAB] results in tropical seabirds being largely represented by Pelecaniformes (boobies, frigatebirds etc) whereas polar and cool temperate seabirds mainly comprise Procellariiformes (petrels, albatrosses) and penguins. Conclusions deriving from comparisons between such different assemblages of species, particularly in the absence of data for tropical Procellariiformes and penguins, are likely to inappropriate and misleading.

Furthermore, attention should be drawn to certain errors of omission and commission and to other problems in the data selected for use by Fairbairn and Shine (1993) and also to difficulties inherent in the nature of the available data on seabird mass for analysis of sexual dimorphism. Together, these pose significant potential problems for intra- and inter-species comparisons and the table of sexual size dimorphism values given by Fairbairn and Shine (1993) should not be used without correction and caution.

Nature of data on sexual dimorphism in mass in seabirds

Confining consideration of sexual dimorphism (SSD, defined by Fairbairn and Shine (1993) as: (larger sex divided by smaller sex) −1.0, arbitrarily positive if female

larger, negative if male larger), to mass (and not also considering morphometric characteristics) gives rise to a substantial problem in many seabirds, especially penguins and Procellariiformes. This is because large changes in mass typically occur during the breeding season, reflecting the pattern of pre-laying attendance fasts (especially, or most extensively, by males), lengthy fasting during incubation shifts (by both sexes) and reacquisition of fat reserves to undertake a fast during moult (penguins). Such a pattern of mass change is shown in Fig. 1. In this case, even data from weighing sexes on the same day could produce indices of sexual dimorphism ranging from 0.97 in favour of males to 0.10 in favour of females. Comparisons based on masses of sexes recorded at different (or unknown) times in the season or even combined across the season could obviously contain significant biases and give rise to an even greater potential range of SSD indices.

While the pattern in Fig. 1 is typical of all crested (*Eudyptes*) penguins, not dissimilar patterns of change in sexual dimorphism index were reported by Ainley and Emison (1972) for Adelie penguins *Pygoscelis adeliae* and also apply generally to all penguins (least so in the case of the gentoo penguin *Pygoscelis papua*) and, except for the massive pre-moult fattening, also to Procellariiformes (see e.g. Prince et al. 1981). In comparing masses between sexes and species great care is needed to ensure that the data used derive from comparable stages of the breeding season and/or represent birds at equivalent stages of breeding.

Against this background, the data from HANZAB used by Fairbairn and Shine (1993) can be assessed. For penguins these can be summarised as follows:

1) king penguin *Aptenodytes patagonicus*: a) breeding, b) pre-breeding; 2) emperor penguin *A. forsteri*: during moult; 3) Adélie penguin *Pygoscelis adeliae*: first arriving pre-breeders; 4) chinstrap penguin *P. antarctica*: a) on one day during chick rearing, b) over 3–4 weeks in
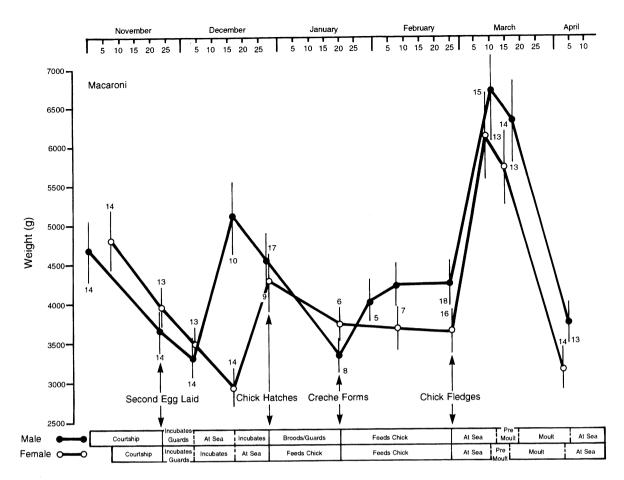
Fig. 1. Mass changes during the breeding season in macaroni penguins at South Georgia (modified from Croxall 1984).

chick rearing; 5) little penguin *Eudyptula minor*: unknown; 6) gentoo penguin: unspecified breeders; 7) yellow-eyed penguin *Megadyptes antipodes*: pre-moult; 8) Fiordland penguin *Eudyptes pachyrhynchus*: pre-moult; 9) erect-crested penguin *E. sclateri*: pre-moult; 10) royal penguin *E. schlegeli*: unspecified breeders without sample size; 11) rockhopper penguin *E. chrysocome*: a) breeders over a 3 week period, b) to d) breeders weighed on a single day.

Realistic comparisons across species, even within genera, are therefore rather difficult given the often radically different status of the birds involved. Even within species, most of the potential biases noted above are likely to apply, in that birds of different sexes could be at different stages of losing or acquiring body reserves, even if weighed on the same day and especially so for events (like arrival to breed and moult) where sexes characteristically have different timings.

The problems are probably less severe for Procellariiformes, which show less variation in mass during the breeding season than penguins. However two additional

problems peculiar to petrels in Fairbairn and Shine's (1993) analysis are the use of data from beach cast specimens and from museum skins. Beach cast material (the only data for Kerguelen petrel *Pterodroma brevirostris*, blue petrel *Halobaena caerulea*, Buller's shearwater *Puffinus bulleri*, fluttering shearwater *P. gavia*, sooty shearwater *P. griseus*), besides deriving from birds of unknown provenance and status (reducing reliability for inter-sex comparisons), is consistently about 75% of the mass of live birds, thus further biasing interspecies comparisons. Most mass data from museum skins used in Fairbairn and Shine's (1993) study had little or no information on status and even date was sometimes unrecorded. Further, to obtain adequate samples, HANZAB often lumped material from several different sites. The potential biases introduced by the various combinations of data from live, beach cast and museum specimens needs to be taken into account when making inter- and intra-specific comparisons.

Finally, there are numerous errors in the data presented by Fairbairn and Shine (1993), including the selection from HANZAB of only some (and often not the most

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representative) data for some species and excluding other species. These errors and omissions are summarised in the Appendix.

Conclusions from data

On examination of the data presented by Fairbairn and Shine (1993 Table 1), and taking into account the corrections and additions available (Appendix), one obvious feature, but not even referred to by Fairbairn and Shine (1993), is that certain species-groups have fairly consistent patterns of sexual size dimorphism in respect of mass. These patterns are, broadly, consistent with those recognised, explicitly or implicitly, in the existing literature on the subject (e.g. Ainley and Emison 1972, Jouventin and Mougin 1981, Croxall 1982, Jouventin and Viot 1985, Warham 1990).

Thus, a) Sulidae (but possibly not gannets *Morus* spp) and Fregatidae have females larger than males; b) Phalacrocoracidae have males larger than females; c) Spheniscidae have males larger than females; the dimorphism is most obvious in the medium-sized crested penguins (*Eudyptes*) and least in *Pygoscelis* and *Spheniscus* species; d) Hydrobatidae consistently have females larger than males; e) Diomedeidae have males larger than females, especially in the great albatrosses; f) Procellaridae show a fair degree of variation (perhaps not surprising considering the diversity of the family) but broadly speaking the fulmarine petrels (and especially the giant petrels) have males significantly larger than females (though Antarctic petrel may need further study) and in most remaining groups (e.g. prions, gadfly petrels, shearwaters) the sexual dimorphism is relatively small and any substantial departures (see Appendix) warrant careful re-examination.

On this basis we can re-examine Fairbairn and Shine (1993) original conclusions. First, that sexual dimorphism is related to body size with larger species showing greater male-biased dimorphism. I contend that the overall relationship (all species combined) simply reflects that the lightest seabirds (storm petrels) show consistently high female-biased sexual dimorphism and that the heaviest ones (albatrosses, giant petrels) show the greatest male-biased sexual dimorphism. Even so the overall relationship accounted for only 16% of the variation – in large part because the medium-to-large boobies and frigate birds show female-biased sexual dimorphism. This suggests that cross-order statistical comparisons may not be a particularly fruitful way to examine sexual dimorphism in seabirds; it might be more useful to investigate why certain groups show consistent female bias in sexual size dimorphism and why (or whether) other groups have species which do not fit the general pattern for that group.

Second, that female-biased sexual dimorphism is greater in areas of poorer productivity (i.e. in the tropics). I

suggest that this apparent relationship simply reflects the different composition of the seabird fauna associated with each of the three different levels of carbon fixation. Thus all boobies and frigate birds, two of the three groups which show consistent female-biased sexual dimorphism, are associated with the tropics and thereby low values of carbon fixation. In contrast, all albatrosses, most penguins and petrels (all groups showing male-biased sexual dimorphism) are associated with high values of carbon fixation. This situation in part results from using a single source work (HANZAB) devoted to a region most of whose seabirds (particularly in the groups investigated – which excluded gulls and terns) inhabit cool temperate, subantarctic and Antarctic waters. However, additional data for tropical species (e.g. *Spheniscus* penguins) and *Pterodroma* and *Puffinus* petrels; see Harris 1969, 1970) could readily have been included. These species all show male-biased SSD's typical of their groups, rather than female-biased SSD's as predicted by Fairbairn and Shine (1993). Therefore I believe their result to be an artefact of the species available, or selected, for analysis, rather than any systematic effect across seabirds, or within particular seabird taxa, which can be related to ocean productivity.

Sexual dimorphism in seabirds

I believe that 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 primary productivity. However, as Fairbairn and Shine (1993) indicate, little research has been specifically directed at this topic. Nevertheless, at least for penguins and petrels, some relevant data do exist on which various hypotheses have been advanced. First, scope for greater sexual dimorphism is undoubtedly enhanced by larger body size (see Clutton-Brock et al. 1977), particularly where small size can confer energetic disadvantages. This may explain why the large seabirds (Sulidae, Fregatidae, Diomedeidae, Phalacrocoracidae, giant petrels) show greater dimorphism, though without explaining its functional significance in these groups.

The implications of small size may also be relevant to the reversed sexual dimorphism in storm petrels. Within Procellariiformes, storm petrels have the largest eggs in proportion to their body mass, as part of the strong general relationship across the whole order (see Croxall 1984, Fig. 10). One of the consequences of forming and laying an egg that is over 25% of adult body mass may be selection for increased female size to facilitate this.

Most studies of sexual dimorphism in penguins and petrels have focused on relationships with prey size, type and foraging area. There is good evidence for intersexual differences in diet in giant petrels (Hunter 1984), wandering albatrosses (J. P. Croxall unpublished data) and for small scale differences in prey size in various penguin taxa (e.g. Ainley and Emison 1972, Croxall and Prince

1980). The only suggestion of sex-specific differences in foraging range comes from wandering albatrosses (Weimerskirch et al. 1985, Prince et al. 1992). For snow petrels, the unusually large dimorphism may in part reflect the complex evolutionary history of this species with potential secondary introgression of two taxa of very different size (Jouventin and Viot 1985). All this suggests that a variety of different processes may contribute to the observed patterns of sexual size dimorphism in Southern Hemisphere seabirds. It also testifies to the need for more comprehensive and detailed field studies of this topic in seabirds generally.

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Appendix

Sexual size (mass) dimorphism in South Hemisphere seabirds. Corrections and additions to and comments on data used by Fairbairn and Shine (1993). All unreferenced sources can be located in HANZAB.

Spheniscidae
Eudyptes chrysocome Rockhopper penguin: Third line (Antipodes Island) should be: males 2430 g, females 2230 g, SSD = −0.09, not 3420 g, 2230 g, SSD = −0.53.

Eudyptes chrysolophus Macaroni penguin
Omitted, despite extensive published data (see e.g. Croxall 1984).

Eudyptula minor Little penguin
Data used are for a sample of n = 5 of each sex of unknown date; information based on 23,000 sexed birds is not used.

Diomedeidae
Diomedea exulans Wandering albatross
Of the two sets of data used one is from breeders, the other from non-breeders.

D. melanophris Black-browed albatross
Data for *D.m. impavida* (SSD = −0.15) excluded; data for *D.m. melanophris*, standardised for status and date (SSD = −0.22) (Prince et al. 1981), excluded.

D. chrysostoma Grey-headed albatross
Data standardised for status and date (SSD = −0.16) (Prince et al. 1981) are excluded.

D. bulleri Buller's albatross
Data for *D.b. platei* excluded (SSD = −0.17).

Phoebetria palpebrata Light-mantled sooty albatross
Species excluded. Although the HANZAB sample is small (n = 3, 5) samples of this size were included for *Procellaria cinerea*, *Pterodroma cervicalis* and *P. solandri*. The HANZAB data give an SSD of +0.05 for *P. palpenbrata*, unique in the family, but this at least highlights a problem to be followed up.

Procellariidae
Daption capense Cape petrel
Data from the Balleny Islands (in HANZAB) are excluded. They give an SSD of −0.06, consistent with other data from distant populations at the South Orkney and Snares Islands.

Thalassoica antarctica Antarctic petrel
Species excluded despite two sets of data (in HANZAB) giving SSD of −0.06 and +0.03, the latter from Terre Adelie (Isenmann et al. 1969), being the only reported incidence of reversed sexual dimorphism in fulmarine petrels. Given that morphometric data show that male Antarctic petrels are significantly larger than females (Lorentsen and Røv 1994), verification is necessary.

Pterodroma solandri Kermadec petrel

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The SSD of −0.22 is based on a small sample (n = 3, 2) and is a much greater difference than would be suggested by the morphometrics of this species.

Pterodroma brevirostris Kerguelen petrel
Data from beach cast specimens give an SSD of +0.11, totally unsupported by morphometrics, which needs verification.

Pterodroma cookii Cook's petrel
Small sample (n = 3, 7) of skins collected over a 5 month period give an SSD of +0.18, inconsistent with the morphometrics of this species and needing confirmation.

Pachyptila turtur Fairy prion
These data, from breeding birds, measured by the same person in the same way, give an SSD in favour of males at the Snares Islands and in favour of females at the Chatham Islands (and 20% smaller at the latter site), despite no similar differences in morphometrics between the two sites. This interesting situation needs further investigation.

Puffinus gavia Fluttering shearwater
The bias in favour of females derives from a very small sample (2 males, 8 females) of beach cast birds.

Pterodroma macroptera Great-winged petrel
Species excluded, despite comprehensive data (summarised in HANZAB) giving an SSD of 0.00. Morphometrics indicate that males might be slightly larger. Note that weights of beach cast birds would have suggested an SSD in favour of females.

Pterodroma inexpectata Mottled petrel
Available data suggest an SSD of +0.11, based on post-breeding birds, but unsupported by morphometric differences which suggest that males are structurally larger.

Procellaria aequinoctialis White-chinned petrel
Data (in HANZAB) from South Georgia give an SSD of −0.09, fitting well with other species of this genus.

Puffinus griseus Sooty shearwater
The small sample (n = 6) gives an SSD of −0.15, fitting well with morphometric data.

Puffinus huttoni Hutton's shearwater
Date from beach cast birds give an SSD of −0.11.

Oceanites oceanicus Wilson's storm petrel
The third line of data refers to grey-backed storm petrels. South Georgia data (Copestake and Croxall (1985) in HANZAB) have been excluded; these show a clear reversed sexual dimorphism (SSD = +0.08).

Oceanites nereis Grey-backed storm petrel
Data combine measurements from three separate localities.

Fregetta tropica Black-bellied storm petrel
Interpopulation comparison is invalid because data compare live birds from one site with skins from three different sites combined.

F. grallaria White-bellied storm petrel
Data from Tristan da Cunha (Hagen 1952, quoted in HANZAB) are excluded and give an SSD of +0.21.

Pelagodroma marina White-faced storm petrel
New Zealand measurements (given in HANZAB) have been excluded; these would give an SSD of +0.36, very different from the +0.03 derived from Australian data. This disparity, which, given the morphometric data, is unlikely to reflect site-specific differences, indicates the potential magnitude of differences due to status, date of measurement etc.