SEXUAL DIMORPHISM IN SNOW PETRELS
Pagodroma nivea

By J. P. CROXALL

ABSTRACT

By means of data in the literature and a large sample of sexed birds from Signy Island, South Orkney Islands, Snow Petrels are shown to be sexually dimorphic in size and especially in body weight and bill length. By these characters alone, over 80% of Signy birds can be correctly sexed.

It is suggested that the true status of the so-called large and small forms of the species can best be resolved by comparing birds of known sex and status. The sexual dimorphism in weight in Snow Petrels is amongst the greatest in the Procellariiformes and might relate to the extensive use of vocalisations in individual and sex recognition.

INTRODUCTION

The range of variation in size of Snow Petrels *(Pagodroma nivea)* at breeding stations on the Antarctic continent has received considerable attention. Prevost (1969) and Isenmann (1970) provided extensive quantitative reviews of the literature and of their own specimens collected in Adelieland and adjacent regions. Prevost (1969) concluded that a large form of the species *(Pagodroma nivea major)* bred in Adelieland and probably at the Balleny Islands and a distinctly smaller form *(Pagodroma n. nivea)* bred elsewhere. A more qualitative review by Cowan (1981) recorded the existence of an apparently intermediate population at Casey and concluded that size variation in Snow Petrels is essentially of a continuous nature and that recognition of infraspecific taxa based on variation in size is not desirable.

None of these authors took into account the marked sexual dimorphism in size in this species, which is clearly of potential importance in this context. My purpose here is to review the nature and extent of this sexual dimorphism, with the aid of recent data from Signy Island, South Orkney Islands (60°43'S, 45°36'W), and to comment briefly on its implications for analysis of morphometric variation in Snow Petrels.

MATERIALS AND METHODS

The data used from the literature are mainly from samples where a reasonable number of sexed mature specimens from a single breeding locality had been measured and where at least the weight, wing length, tarsus and bill length had been recorded. Unfortunately

TABLE 1 — Measurements of Snow Petrels. Mean values with standard deviation in parentheses. Weight in grams; other measurements in millimetres

Location and sample size	Weight			Wing			Tarsus			Bill length			Bill depth			Reference
	Male		Female	Male		Female	Male		Female	Male		Female	Male		Female	
Cape Hunter (3 ♂ 5 ♀)	317 (85)		291 (48)	276 (12)		271 (21)	35.2 (2.7)		34.1 (3.3)	22.5 (1.8)		21.4 (2.0)	11.6 (1.6)		11.7 (1.2)	Isenmann <u>et al</u>, 1969
Cape Denison (7 ♂ 4 ♀)	332 (18)	***	244 (17)	268 (4)	**	255 (5)	33.7 (4.1)		31.6 (1.9)	22.5 (1.1)	***	19.0 (0.8)	11.9 (0.5)	***	10.5 (0.2)	Isenmann <u>et al</u>, 1969
Cape Hallett (10 ♂ 4 ♀)	290 (20)		276 (19)													Maher 1962
Bluff I. (6 ♂ 6 ♀)	268 (19)	*	246 (16)	264 (3)		259 (7)	32.4 (0.8)		32.3 (0.8)	20.9 (0.5)	*	19.8 (0.6)				Brown 1966
Anchorage I. (6 ♂ 6 ♀)	293 (18)	*	246 (21)	264 (4)	*	256 (3)	33.4 (1.5)		32.3 (1.0)	20.5 (0.6)	***	18.8 (0.6)				Brown 1966
Signy Island (18 ♂ 21 ♀)				278 (6)	**	270 (6)	38.2 (1.3)		37.2 (1.2)	22.3 (1.1)	***	20.2 (1.1)				This paper
Adelieland (79-91)	400 (range 242-525)			290 (range 242-320)			37.3 (range 30.0-42.5)			23.8 (range 19.0-27.8)			12.6 (range 9.8-14.7)			Prevost 1969
Casey (178)				c276 (range 240-320)			c36.3 (range 31-44)			c22.1 (range 18-27)						Cowan 1981, Fig. 4

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

in many large samples, especially those from Adelieland and Casey, no attempt was made to sex birds.

At Signy Island, the occupants of up to 50 marked nest sites are all ringed and are checked annually. Many of these birds have been sexed by cloacal inspection, by observed egg-laying, by presence at the nest on the day on which the egg was laid, or by vocalisation (see Isenmann 1970, Guillotin & Jouventin 1980). For ecological purposes (see Croxall & Prince 1980, 1982), some of these birds were measured for weight, bill length and wing area between 2 and 9 January, near the mean date of hatching (8 January), when incubation shifts are short and a good sample of birds of both sexes can be quickly obtained. Other measurements (but not weight) are available for birds measured at various times in several seasons.

Sets of data are compared using 't' tests.

RESULTS

Table 1 gives data from the small samples available of sexed birds from six sites and, for comparison, data for the unsexed samples from the important sites at Casey and Adelieland.

Except for bill depth at Cape Hunter, males are larger than females in all dimensions. The differences are statistically significant most frequently for weight and bill length (four sites); wing length differences are significant at three sites; tarsal length differences are significant only at Signy Island. Based on the Cape Denison sample and Prevost's (1969) comments, bill depth is probably also usually significantly different between sexes.

Data for the Signy Island breeding pairs are given in Table 2. At 19 nests at least one member of the pair was already sexed by

TABLE 2 — Snow Petrel measurements at Signy Island. Conventions as in Table 1

Sample size	Weight			Bill length		
	Male		Female	Male		Female
1. 20♂ 20♀	341	***	293	21.7	***	19.9
	(30)		(25)	(1.8)		(1.5)
2. 23♂ 23♀	339	***	281	21.8	*	20.4
	(20)		(24)	(1.5)		(1.9)
3. 43♂ 43♀	340	***	286	21.7	***	20.1
	(25)		(25)	(1.6)		(1.7)

TABLE 3 — Weights (grams ± one standard deviation) of sexed Snow Petrels from Adelieland. From Guillotin & Jouventin (1980, Table 5)

Sample size	Male		Female
a. 8♂ 9♀	460 ± 43	***	380 ± 42
b. 12♂ 13♀	459 ± 35	***	358 ± 32
c. 9♂ 9♀	443 ± 49	***	339 ± 49

TABLE 4 — Sexual dimorphism index (♀/♂ x 100) of Snow Petrel populations

Site	Weight	Wing	Tarsus	Culmen
Cape Hunter	92	98	97	95
Cape Denison	73	95	94	84
Bluff I.	92	98	100	95
Anchorage I.	84	97	96	92
Signy*	84	97	97	91
Adelieland+ (a)	83			
(b)	78			
(c)	77			

* From Table 1 and Table 2 sample 3

+ From Table 3

the non-mensural characteristics listed above and weight and bill length data were available for both birds of the pair. At two nests the sexed birds, but not their partners, could be caught. These data form sample 1. To increase the sample of reliably sexed birds, individuals at other nests were assigned to a sex only if their weight or bill length exceeded the range of values for the 20 birds of each sex in sample 1. The 23 birds directly sexed in this way will obviously show a bias towards large males and small females. However, the size of the partners of these birds should not be biased in any way. The data for these 23 pairs, which form sample 2, are not statistically different from the birds in sample 1, and they are combined to form sample 3. Except for bill length in sample 2, all differences between sexes are highly significant. Signy birds are all significantly heavier ($p = 0.01 - 0.001$) than those from any other site, except Cape Hunter and except for males from Cape Denison and females from Cape Hallett.

Recent data from Adelieland (Guillotin & Jouventin 1980) show similar highly significant differences in weight between the sexes for three samples from different types of breeding site (Table 3). These birds are very significantly heavier ($p << 0.001$) than those from any site in Table 1, being 25-30% heavier even than Signy birds.

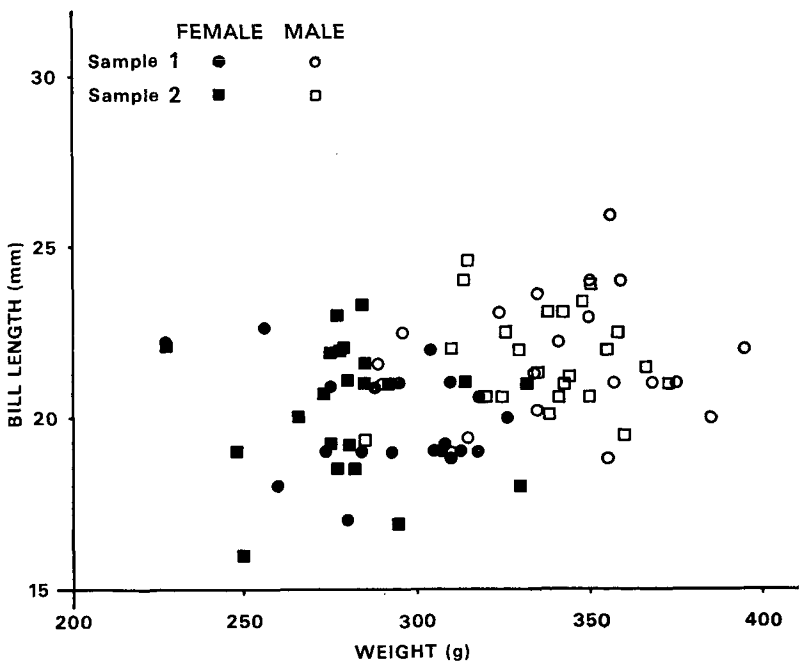

FIGURE 1 — Bill length and weight of sexed Snow Petrels from Signy Island, South Orkney Islands. Sample numbers refer to Table 2.

TABLE 5 — Index of sexual dimorphism in weight for various Procellariiformes

Species	Index	Reference
Northern Giant Petrel *Macronectes halli*	76.3	S. Hunter, pers. comm.
Southern Giant Petrel *M. giganteus*	77.9	Conroy 1972
Wandering Albatross *Diomedea exulans*	78.2 78.7	Croxall & Ricketts in press, Table 3; Tickell 1968
Waved Albatross *D. irrorata*	81.1	Harris 1973
Snow Petrel*	83.0	This paper
Royal Albatross *D. epomophora*	84.4	Sorensen 1950
Northern Fulmar *Fulmarus glacialis*	79.9-84.7	Mougin 1967; Cramp & Simmons 1977
Cory's Shearwater *Calonectris diomedea*	86.5	Zino 1971
Laysan Albatross *D. immutabilis*	87.5	Fisher 1967
Antarctic Fulmar *F. glacialoides*	88.2	Mougin 1967
Grey-faced Petrel *Pterodroma macroptera*	90.2	Imber 1976
Cape Pigeon *Daption capense*	92.1	Pinder 1966
Grey Petrel *Procellaria cinerea*	92.2	Barrat 1974
Sooty Albatross *Phoebetria fusca*	92.3	Berruti 1979
Black-browed Albatross *D. melanophrys*	94.2	Prince *et al.* 1981
Short-tailed Shearwater *Puffinus tenuirostris*	94.3	Palmer 1962
Antarctic Prion *Pachyptila desolata*	95.6	Tickell 1962
Grey-headed Albatross *D. chrysostoma*	96.6	Prince *et al.* 1981
Manx Shearwater *Puffinus puffinus*	97.3	Brooke 1978
Audubon's Shearwater *P. lherminieri*	98.5	Harris 1969
Dark-rumped Petrel *Pterodroma phaeopygia*	99.8	Harris 1970
Great Shearwater *Puffinus gravis*	100.6	Hagen 1952
Black-bellied Storm Petrel *Fregatta tropica*	100.9	Beck & Brown 1971
Leach's Storm Petrel *Oceanodroma leucorhoa*	104.1	Palmer 1962
White-bellied Storm Petrel *Fregetta grallaria*	121.3	Hagen 1952

* Mean weighted by sample size from each site

The degree of sexual dimorphism is summarised as an index in Table 4, where the Bluff Island and Cape Hunter populations stand out as least dimorphic (especially by weight). Weight and bill length are clearly the best discriminators between the sexes.

The use of weight and bill length data in sexing Snow Petrels is shown in Fig. 1, where these characters are plotted together for the Signy Island birds in Table 2, samples 1 and 2. Although there is clearly some overlap between the sexes, weight and bill length alone will allow correct sexing of 85% of the birds. Better discrimination would undoubtedly be achieved by use of a third character, and bill depth is likely to be the best measurement to use.

DISCUSSION

The Snow Petrel shows a remarkable degree of sexual dimorphism in weight, being proportionately one of the most dimorphic species of the Procellariiformes, data for 25 species of which are summarised in Table 5. Snow Petrels are sexually dimorphic in other mensural characteristics, but particularly so in bill length (and possibly bill depth). With the use of weight and bill length, probably over 80% of adult birds at any locality can be correctly sexed. If pairs of breeding birds are measured even better results are likely because at Signy it is very rare for the female of a pair to be larger than her mate. Thus, the smallest male (285 g; bill 19.3 mm) was still appreciably larger than his partner (248 g; 19.0 mm).

Cowan (1981) advocated that wing length should be the main standard for comparison of Snow Petrels. This may be desirable when comparing unsexed material because wing and tarsal length show least differences between sexes, but if birds are to be sexed — and this must surely make comparisons both more accurate and more relevant biologically — a full set of measurements should be made. Undeniably, weight is the most variable measurement, and so it is the more remarkable that the sexual dimorphism in weight of Snow Petrels is so clear. If, however, sampling is restricted to breeding birds, weights will be much more comparable and variations will relate mainly to changes during incubation and chick rearing. As Snow Petrels do not undertake particularly long incubation fasts, with mean values over all shifts 3-6 days (Mougin 1968, Isenmann 1970), the mean weight loss per day at this time would be about 7 g (Croxall 1982) and this degree of weight variation is unlikely to cause serious problems with comparing and analysing data.

Wing length, being invariably the longest linear measurement made, is perhaps the most accurate, but in other studies of Procellariiformes it is also a poor indicator of sexual differences (see Tickell 1968 Table 4, Conroy 1972 Table 4 — but note that in this the mean female wing length is incorrect, as are most 't' values —, Brooke 1978). Despite their small absolute size, bill dimensions are commonly used to sex a wide range of seabirds, e.g. Northern Fulmar (Dunnet &

Anderson 1961), Wandering Albatross (Tickell 1968, Fig. 9), Southern Giant Petrel (Conroy 1972, Fig. 2), various penguins (e.g. Warham 1975) and shags *Phalacrocorax* spp. (J. C. Coulson, P. Shaw, pers. comm.), and they appear to be equally useful in the Snow Petrel.

What significance, then, does the recognition of substantial sexual dimorphism in Snow Petrels have for interpreting their morphometric variation? If we take first the accepted view (i.e. before Cowan 1981) that a large form breeds in Adelieland and a smaller one elsewhere, then Guillotin & Jouventin's (1980) graph of the distribution of wing length measurements portrays this situation adequately by showing two distinctly separate peaks but with substantial overlap. Recognition of the degree of sexual dimorphism (even in wing length) means that most overlap consists of large males of the small-sized population and small females of the large-sized population. Thus the two populations are much more distinct than hitherto appreciated.

The nature of the population at Casey, however, complicates matters and it is unfortunate that weight data are lacking and that precise summary statistics are not explicitly stated and have to be derived from text-figures. In mean wing length, Casey birds are close to the small Signy sample and about twice as close to the smaller-sized populations than to the Adelieland birds. If they have similar body mass to Signy birds, the disparity in this character from Adelieland birds is greater still. If this was all, we might still conclude that the overlap between Casey and Adelieland birds was the product of large males from one and small females from the other. However, as Cowan (1981) recognised, the ranges of values for all linear measurements from Casey are virtually identical to those from Adelieland, and it is principally the 'centre of gravity' of the populations that seems to be so distinct. The situation at both sites should clearly be examined using only sexed birds of known reproductive status.

If birds of the same sex and status at Casey and Adelieland do prove to span a similar size range, yet the bulk of birds at each site is significantly different in most dimensions, this will be difficult to treat taxonomically but important to study to find out how the situation is maintained and its adaptive significance. Such a study would necessarily involve examining the mating system in the species and looking at the relationship between female dimensions and egg size, hatchling size (usually strongly correlated with egg size — see Croxall, in press) and fledgling size. Although Isenmann (1970) suggested that birds of different sizes favoured different nesting sites, Guillotin & Jouventin's (1980) data did not support this, and habitat differences between Adelieland and Casey are unlikely to be responsible for the morphometric differences of the birds there.

Why Snow Petrels show high sexual dimorphism is still not clear. In Wandering and Royal Albatrosses at least, dimorphism may have arisen by sexual selection operating through the potential for mate selection offered by the aggregation at display sites of large numbers of immature birds of both sexes. In giant petrels, the dimorphism may be significant in terms of the different feeding strategies of the sexes (S. Hunter, in prep.) and may have arisen through conventional *intra*-specific competition for food.

Neither explanation seems particularly plausible for Snow Petrels. Guillotin & Jouventin (1980) showed that in Snow Petrels body weight is correlated with the sound frequency of vocalisations. Both they and Isenmann (1970) emphasised the extensive role that vocalisations play in recognition of individuals and sexes in this species. In a species so entirely devoid of plumage marking, selection may have favoured the increased development of sexual dimorphism as a simple way of increasing the range of vocal frequencies available within the sexes of a population in order to provide the scope for an extensive intraspecific repertoire, given the very limited variations in phrasing that most Procellariiformes seem able to produce.

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J. P. CROXALL, *British Antarctic Survey, Natural Environment Research Council, Madingley Road, Cambridge CB3 OET, United Kingdom*

SHORT NOTE

TUI FEEDING ON SANDHOPPERS

On 6 December 1981 at the mouth of Sealers Creek on Codfish Island, northwest of Stewart Island, I saw a Tui fly from the adjacent muttonbird scrub and land on the wet sand beside the creek at low tide. The Tui moved around on the sand catching sandhoppers both on the surface and also by probing into the firm sand. This unusual behaviour lasted for about 3 minutes before the Tui flew to a stand of flax which was not then in flower. Inspection of the area where the Tui had been feeding revealed footprints and shallow probe holes over an area of about 4 m^2. Unidentified sandhoppers were numerous both on the surface and in the wet sand. The same feeding behaviour was observed again at low tide on the following day, but on this occasion the Tui, possibly the same bird, fed only briefly on surface sandhoppers before flying off. Tuis, like Bellbirds, have a broad diet of insects, fruits and nectar, but the taking of small marine crustacea from sand below high water is surprising and demonstrates the adaptability of this New Zealand honey-eater.

M. J. DANIEL, *Ecology Division, DSIR, Lower Hutt*