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Identification and breeding biology of the diving petrels *Pelecanoides georgicus* and *P. urinatrix exsul* at South Georgia

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The biology of two species of diving petrel (*Pelecanoides georgicus* and *P. urinatrix exsul*) was studied at Bird Island, South Georgia. Existing criteria (bill shape and morphology, wing length) for distinguishing these species are reviewed, and several new characters are recognised. For adults bill depth, the colour of the posterior part of the tarsus, and vocalisations are distinctive; chicks have down of different colours (pale grey in *P. u. exsul*, dark grey in *P. georgicus*). At South Georgia the species breed in different habitats and at different times - *P. u. exsul* nests in steep tussock slopes in very early summer, *P. georgicus* in fine scree slopes in midsummer. *P. georgicus* lays a proportionately larger egg, and has an incubation period of 46 days (c.54 days in *P. u. exsul*) and a chick fledging period of 46 days. The fledging period of *P. u. exsul* is 54 days, very similar to recorded values for *P. u. urinatrix* (53.5 days) and *P. u. chathamensis* (56 days). Data on feeding frequency and feed size were derived from daily chick weighings and from twice-daily weighing during 30 days preceding fledging. In both species chicks are fed every night, and often by both parents. In *P. georgicus* true mean chick feed size is c.37 g; in *P. u. exsul* it may be slightly less. Analysis of chick stomach contents suggests that *P. u. exsul* feeds extensively on copepods, whereas *P. georgicus* largely takes krill (*Euphausia superba*). *P. u. exsul* breeding adults commence moulting before their chicks have fledged; *P. georgicus* moults exclusively in the non-breeding season. Ectoparasites were collected, and the feather louse *Pelmatocerandra setosa* was found to be restricted to *P. u. exsul*, and *Pelmatocerandra enderleini* to *P. georgicus*. *P. georgicus*, which breeds later and whose chicks fledge faster, is suggested to be better adapted to the climatic and marine environmental conditions than *P. u. exsul*, which may be the more recent colonist of these high latitudes.

INTRODUCTION

In their morphology, behaviour at sea, breeding habits, and wing loading diving petrels have many affinities with the small alcids of the Northern Hemisphere, which are their ecological counterparts (Murphy & Harper 1921, Thoresen 1969, Warham 1977). Genus *Pelecanoides* occurs from southern sub-tropical to Antarctic waters, but the breeding biology of only one of the four species (*P. urinatrix*) has been studied, in two investigations of different subspecies in the New Zealand subregion (Richdale 1943, 1945, 1965, Thoresen 1969). The present study concerns the breeding biology of the South Georgian diving petrel (*P. georgicus*) and the common diving petrel (*P. urinatrix exsul*) at South Georgia, and seeks to identify some of the ways in which the species are separated ecologically.

South Georgia (54°S, 36°W) is a mountainous island some 160 km long by up to 50 km wide lying about 200 km south of the Antarctic Convergence in the South Atlantic. The surrounding waters, on which the extremely numerous seabirds of the region depend, are influenced primarily by the west wind drift from the Bellingshausen Sea and by the Weddell Sea gyre (Hardy 1967). The mixing of these two

cold currents contributes to the high productivity of the seas around South Georgia, and governs the climatic conditions on the island. About 50% of the land surface is covered with permanent ice and snow, and much of the rest is steep rock. Large numbers of birds breed almost exclusively below about 500 m a.s.l. in the narrow coastal belt and on offshore islands, almost all in the predominantly snow-free months of November-April. Rats have been introduced to the main island of South Georgia, and may contribute to the paucity of small petrels there compared with the offshore islands.

This study was carried out on Bird Island (area 500 ha), off the western tip of South Georgia. We were present for three consecutive summer seasons from 1971-72, usually from about mid November until the end of March. It was not until late in the second season that we located a *P. u. exsul* colony, and most of the work was carried out in the final season. The growth of our small sample of *P. u. exsul* chicks, which suffered heavy predation, was rather erratic, and we arranged for this aspect of the work to be repeated in 1975-76.

Time for field study was strictly limited, and initially we had intended to confine ourselves to collecting

breeding birds from their colonies at intervals through the season, with the intention of identifying the main differences in their breeding biology. However, we were able later to make serial observations on selected nests to measure chick growth and determine some of the other breeding parameters. We gathered information on food and feeding of the chicks, but were unable to pursue this topic further.

TAXONOMY AND IDENTIFICATION

The similarity of the diving petrel species in both plumage and morphology makes their identification difficult. The first review of the group was by Murphy & Harper (1921), who classified them largely on the basis of bill structure. Their work was combined with more recent information by Bourne (1968), who arranged the genus into four species on the strength of more complete data on size and distribution, but proposed no further criteria for identification. These four species fall into two groups. One consists of three monotypic species which occupy latitudinally distinct ranges (Fig. 1), one circumpolar in the subantarctic region, the other two occurring in South America, as far north as 6°S. The other group contains a single species (*P. urinatrix*) divided into three or four subspecies, which together parallel the ranges of the species in the first group; however, the northward extension is confined to the New Zealand region. *P. georgicus* is the southernmost and smallest of the three monotypic species, and *P. u. exsul* is the southernmost but intermediate-sized representative of *P. urinatrix*. Both breed at South Georgia, the Prince Edward Islands, the Crozet Islands, Kerguelen, Heard Island, the Auckland Islands, and probably Macquarie Island. *P. u. exsul* also breeds at the Antipodes Islands. They are thus substantially sympatric, and criteria for separating them are of some importance

in view of the confusion that still exists. The main criteria suggested by Murphy & Harper, and by most subsequent authors, are as follows.

- BILL SHAPE:** *P. georgicus* – bill proportionately wider at base and tapering more sharply than in other Pelecanoididae (best seen from underside of lower mandible); *P. u. exsul* – rami of lower mandible nearly parallel, meeting in a Roman arch, not a pointed one.
- PARANASAL PROCESSES:** *P. georgicus* – processes dividing each nostril attached at longitudinal centre of internasal septum (see Murphy & Harper 1921, fig. 2, p. 502); *P. u. exsul* – processes attached at posterior part of internasal septum.
- SIZE:** some individuals can be separated on size alone – *P. u. exsul* tends to be the larger, as shown in Table 1.

Unfortunately, a proportion of individuals cannot be easily identified on these criteria, and accordingly we have assessed a range of characters.

ADULT MEASUREMENTS

We have measured substantial samples of both species. Many birds were caught around the lights of the Bird Island base on foggy nights, but the majority were newly fledged juveniles. For biometric description of the South Georgian populations, therefore, we present in Table 1 the measurements of our adult specimens. These were taken from occupied nests, and are known to be of breeding status. The measurements taken were wing length (maximum chord method, taking the closed wing and gently straightening it along a stopped steel rule); tail length (from the insertion of the central pair of feathers to the tip of the longest); exposed culmen (from the end of the feathers on the top surface of the upper mandible to the tip); bill width (level

Table 1. Dimensions (mm) of *Pelecanoides georgicus* and *P. urinatrix exsul*: mean \pm standard deviation, and range (in parentheses).

	<i>n</i>	Wing length	Tail length	Exposed culmen	Tarsus length	Source
<i>P. georgicus</i>						
South Georgia	50	118.2 \pm 3.21 (112–124)	39.67 \pm 2.26 (34.0–44.0)	14.69 \pm 0.83 (13.4–16.0)	23.77 \pm 0.83 (22.0–26.3)	This study
South Georgia	185	113.2 (104–122)	37.93 (34–43)	14.81 (14–16)	24.31 (21–26)	Murphy & Harper (1921)
South Georgia	13	116 \pm 2.9 (110–120)	39.1 \pm 2.1 (35–43)	15.3 \pm 0.63 (15–17)	24.7 \pm 0.93 (23–26)	Bourne (1968)
Kerguelen I.	27	119.0 \pm 2.61 (115–125.5)	41.07 \pm 1.82 (35–44)	15.11 \pm 0.57 (14–16)	23.31 \pm 1.28 (20–25)	Paulian (1953)
<i>P. u. exsul</i>						
South Georgia	36	124.1 \pm 2.61 (120–130)	40.2 \pm 2.30 (34.5–45.0)	16.25 \pm 0.55 (15.0–17.4)	26.78 \pm 1.00 (24.2–29.1)	This study
South Georgia	13	120 \pm 3.5 (116–124)	38.9 \pm 2.30 (37–40)	16.25 \pm 0.55 (15–18)	26.78 \pm 1.00 (25–27)	Bourne (1968)
Kerguelen I.	10	122.95 \pm 2.28 (119–125)	40.4 \pm 1.11 (38–42)	16.2 \pm 0.78 (15–17.5)	25.36 \pm 0.78 (23.5–26)	Falla (1937)

with the end of the feathers on the top of the upper mandible); bill depth (immediately anterior to the external nares); and tarsus length.

Our values for wing length are larger than all except those of Paulian (1953), who also measured breeding adults only, so this may be due to the inclusion of subadult birds in other collections. Bourne (1968) notes that many of his measurements

were of birds taken at artificial lights on dates consistent with the peak fledging periods of the two species. The mean wing lengths of *P. georgicus* and *P. u. exsul* chicks the evening before fledging—i.e., within a few hours of when they could be caught at lights—were respectively 111 mm (range 107–116 mm; $n = 18$) and 117 mm (range 110–122 mm; $n = 11$). These figures are both 7 mm less than the mean

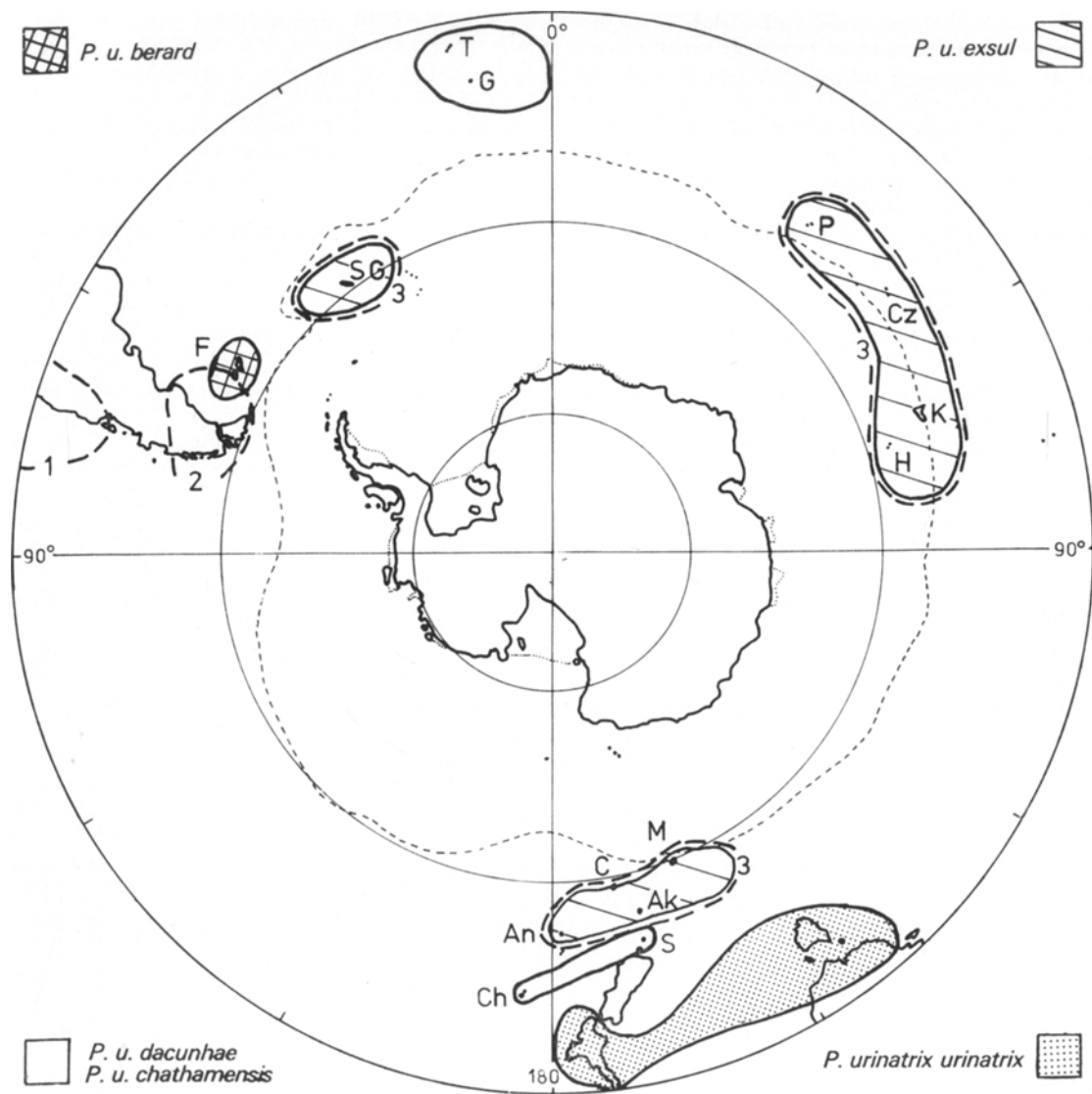


Fig. 1. Distribution of diving petrels, mapped on south polar projection. LOCALITIES: AK, Auckland Is; AN, Antipodes Is; C, Campbell I.; Ch, Chatham Is; Cz, Crozet Is; F, Falkland Is; G, Gough I.; H, Heard I.; K, Kerguelen I.; M, Macquarie I.; P, Prince Edward I. & Marion I.; SG, South Georgia; Sn, The Snarres Is; T, Tristan da Cunha. TAXA: ---1---, *Pelecanoides garnoii*; ---2---, *P. magellani*; ---3---, *P. georgicus*.

wing lengths we obtained for breeding adults. The *P. georgicus* series from which Murphy & Harper's measurements were derived was obtained before the chicks fledged. However, the source of their birds is unspecified, and may have been at sea or on the surface in the colonies; either source could have allowed non-breeding and immature birds to enter the sample. This is demonstrated by our capture of 20 *P. georgicus* on the surface in a colony towards the end of incubation. Thoresen (1969) reported that in *P. u. urinatrix* the brood patch takes 35–40 days to refeather, yet 8 of these 20 had no brood patches, so presumably were not breeding. The mean wing length of the eight was 110.3 mm, compared with 115.3 mm for the birds with brood patches. Thus, inclusion of a substantial proportion of non-breeding birds may depress the mean wing length of a sample. Falla (1937) commented on the small wing length of Murphy & Harper's sample when reporting a mean of 117.7 mm for seven probably breeding birds from Kerguelen. More detailed comparison of the measurements in Table 1 might not be valid, since they derive from fresh birds, specimens preserved in spirit, and dried skins, and there are likely to be significant differences in the measurements of a specimen between the fresh and preserved states.

Wing length varies slightly with sex. Murphy & Harper reported that females of *P. georgicus* were 1.1 mm larger than males in a large sample, and we found confirmed breeding adult females to be 2.7 mm larger. This evidence suggests a small but real difference between the sexes in *P. georgicus*. However, we found little difference in the 10 sexed *P. u. exsul* at our disposal, and Murphy & Harper found none in the specimens they examined.

In view of the importance attached to bill shape and structure, we measured its length, width, and depth (Table 2). Bill depth was found to be the one character of all those measured for which there was no overlap between the species. This is also reflected in Murphy & Harper's data, but attention has not previously been drawn to this character, to which we attach considerable value as a criterion

separating adult *P. georgicus* from adult *P. u. exsul*.

The weight of adult diving petrels fluctuates considerably during the breeding season, as shown by Thoresen (1969) for *P. u. urinatrix*. The most important cause of these fluctuations is probably the energetic requirement of breeding. Our data for the three seasons of the study are combined in Table 3. Both species show an increase in weight after egg-laying (perhaps recovering from the demands of egg formation) followed by a steady decline until the chick fledges. This decline begins during incubation in *P. georgicus*, and may do likewise in *P. u. exsul*. In comparing the two sets of data, allowance must be made for the different breeding seasons of the two species (see Table 8) and a smaller difference between years within each species (see page 310).

PLUMAGE AND SOFT PARTS

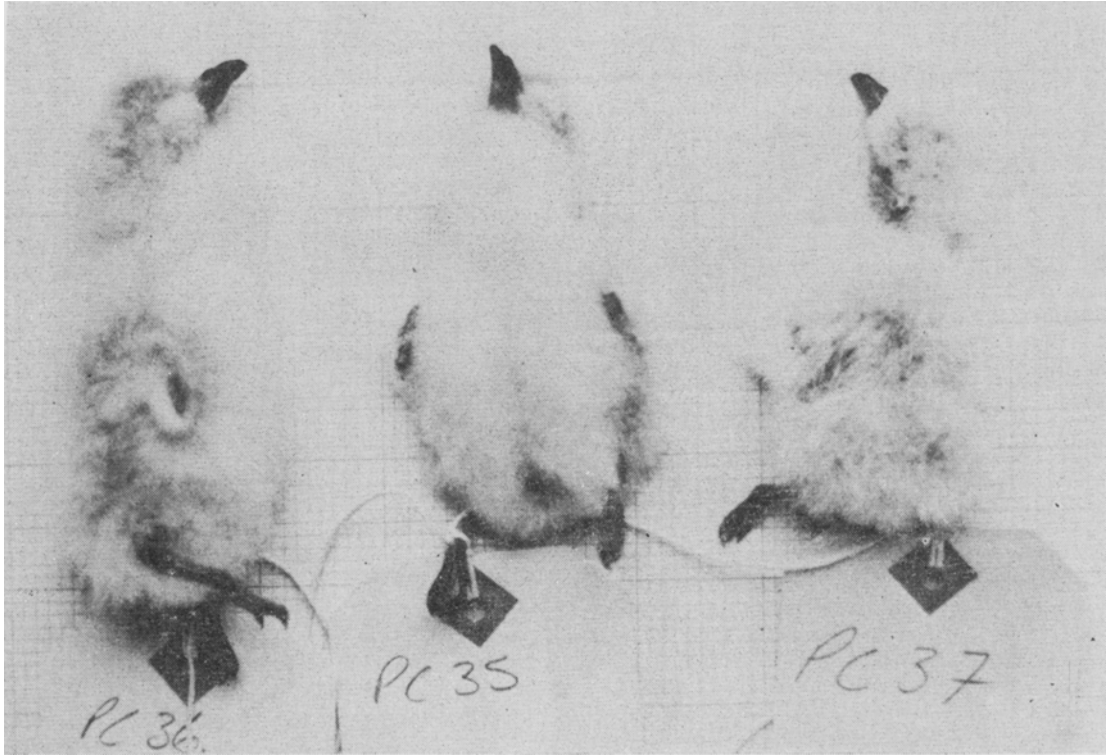
The chicks of the two species are easily separated. That of *P. u. exsul* is clad in very pale down similar to that described by Thoresen (1969) for *P. u. urinatrix*, though it lacks the wedge of darker down round the vent. It remains very pale at all stages (Fig. 2a). The down of *P. georgicus* chicks is a much darker, almost sooty grey throughout (Fig. 2b), and is rather denser than that of *P. u. exsul*.

The adults are extremely similar, but in the past a number of plumage characters have been described as useful in the identification of these two diving petrels, the only ones that occur in Antarctic waters (Falla *et al.* 1966, Watson 1975). We have examined three of these characters critically in 14 *P. georgicus*. We have found that the scapulars of either species may appear to be pale according to the 'lie' of the feathers, which may alter as the bird moves.

The colour of the underwing coverts and the inner webs of the primaries is another frequently cited character. We have found that both are white, or sometimes very pale grey, in *P. georgicus*, whereas *P. u. exsul* has grey underwing coverts with dark shafts and darker inner webs to the primaries. We observed no exception to this, and it appears to be a useful identification feature for birds in the hand,

Table 2. Bill dimensions (mm) of *Pelecanoides georgicus* and *P. urinatrix exsul* from South Georgia: mean, range (in parentheses), and sample size (in *italics*).

Murphy & Harper (1921)		This study	Murphy & Harper (1921)		This study
<i>P. georgicus</i>			<i>P. u. exsul</i>		
Length	♂ 14.9 (14–16) ♀ 14.7 (14–16)	14.7 (13.4–16.0) 50	16.2 (15.5–17) 16		16.3 (15.0–17.4) 36
Width	♂ 8.9 (8–10) ♀ 8.8 (8–9.5)	8.3 (7.4–9.0) 14	8.9 (8.5–9.5) 9		8.5 (7.5–9.8) 25
Depth	♂ 5.8 (5.5–6) ♀ 5.7 (5–6)	5.3 (5.0–5.7) 14	7.1 (6.5–8) 6.7 (6–7)		6.5 (6.0–7.3) 25

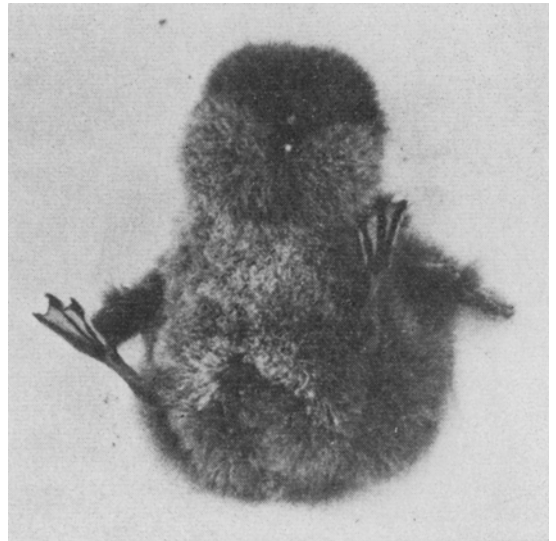


(a)

Fig. 2. Plumage of *Pelecanoides* chicks: (a) *P. urinatrix exsul*, 3–7 days old – note pale-grey down below, darker above, and absence of dark area around vent (cf. Thoresen (1969) for *P. u. urinatrix*); (b) *P. georgicus*, 4 days old – note dense, dark-grey down, darker on crown, and black line developing on rear of tarsus.

Table 3. Weights (g) of breeding adult *Pelecanoides* diving petrels from South Georgia: mean \pm standard deviation, and sample size (in italics).

	<i>P. georgicus</i>	<i>P. u. exsul</i>
8 Dec 1973	107.4 \pm 1.96 5	140.8 \pm 8.86 6
23 Dec 1973	122.8 \pm 13.4 4	149.3 \pm 13.3 6
5 Jan 1974	no data	132.7 \pm 11.3 6
15 Jan 1974	117.0 \pm 10.7 5	126.9 \pm 7.90 7
31 Jan 1973	115.4 \pm 9.65 5	no data
4 Feb 1973	114.8 \pm 7.78 6	130.2 \pm 9.55 6
10 Feb 1973	104.8 \pm 6.72 6	123.0 \pm 7.18 4
20 Feb 1972	105.1 \pm 6.13 12	no data
24 Feb 1973	96.5 \pm 2.99 6	no data
19 Mar 1973	93.3 \pm 3.64 6	no data



(b)

though difficult to see in the field.

The degree of mottling on the breast, throat, and flanks is the third character we have examined. It appears that either species may have a complete or broken breastband, although on average *P. u. exsul* does tend to be rather darker. The flanks too are variable, tending to be darker in *P. georgicus*. Neither character appears to be of value in identification.

While identifying live birds at South Georgia, one of us (P.A.P.) noticed a distinction in tarsus colour (see Fig. 3). The front and sides are consistently pale to lavender blue, but in some birds the rear is black, forming a stripe from 'knee' (intertarsal joint) to 'ankle' (metatarsophalangeal joint). In the adult the black line is restricted to *P. georgicus*. Chicks of both species have little or no line when they hatch, but subsequently develop it. However, in *P. u. exsul* the

line regresses, usually (but not always) by the time of fledging. Normally, only black spots at the rear of the knee and ankle remain. Around New Zealand the same situation exists in *P. u. urinatrix* at the Mercury Islands (A.C. Thoresen, *in litt.*) and in *P. u. chathamensis* (equivalent to Bourne's *P. u. dacunhae*) near Stewart Island (Richdale 1965). There are museum specimens of *P. urinatrix* subspecies described as possessing the black line, for example three birds recently collected at Campbell Island (F. C. Kinsky, *in litt.*). It is possible that such birds are juveniles that have not yet lost the black line, but the situation may well be more complex than it now appears among the subspecies and populations of *P. urinatrix*. As regards *P. magellani* and *P. garnoti*, there is adequate information on the labels of some specimens in the British Museum, and

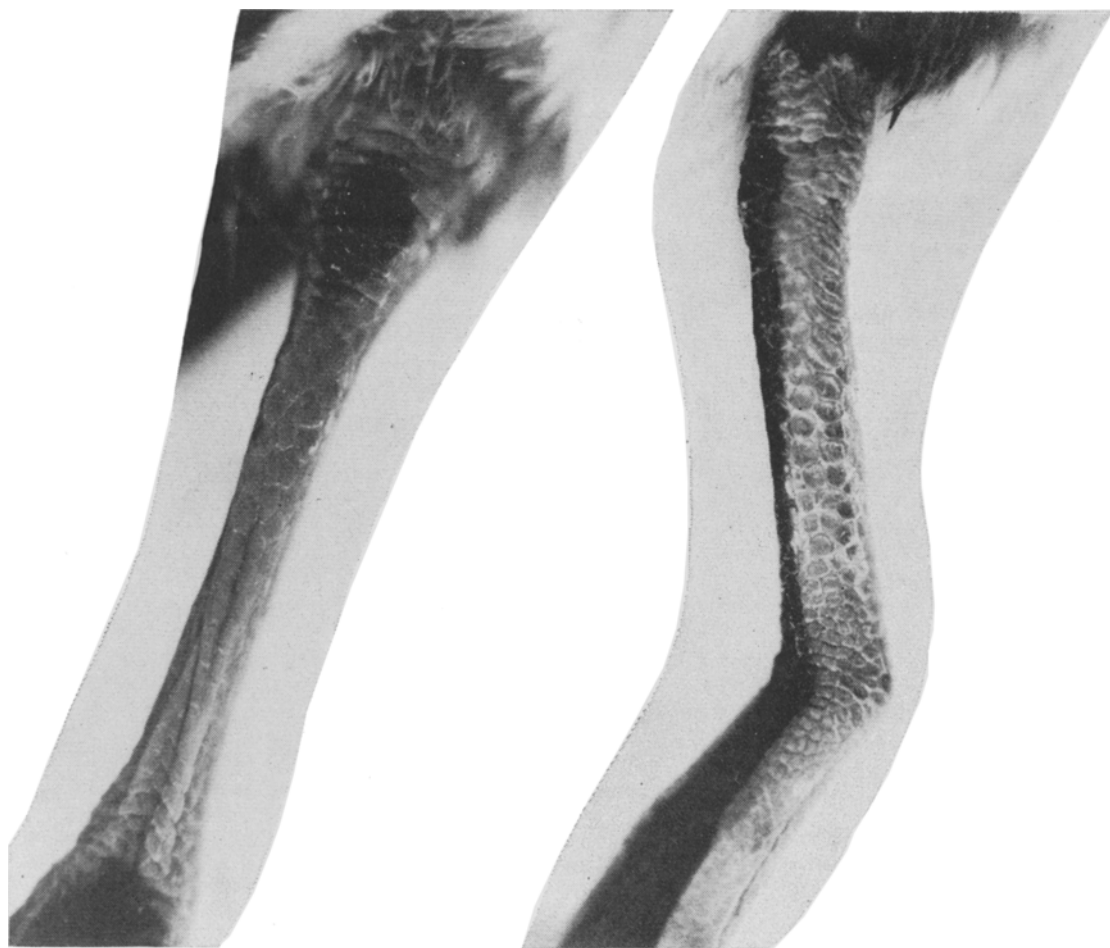


Fig. 3. Tarsus of breeding adults of *Pelecanoides*: (a) *P. urinatrix exsul* - posterior view, showing black coloration at joints only; (b) *P. georgicus* - lateral view, showing continuous black line.

Table 4. Main identification criteria for *Pelecanoides georgicus* and *P. u. exsul*, as determined from material taken at South Georgia.

Character	<i>P. georgicus</i>	<i>P. u. exsul</i>
Wing length (mm)		
Adult	112–124	120–130
Juvenile	107+	110+
Bill depth anterior to nares (mm)	5.0–5.7	6.0–7.3
Rami of lower mandible	Converging	Parallel
Paranasal processes	Medial	Posterior
Underwing coverts	White or very pale grey	Darker grey, shafts dark
Tarsus	With posterior black line	No black line

the legs still retain sufficient traces of bicoloration, to indicate that the black line occurs normally in both species. The character was described by Nicoll (in the simplest interpretation, the character may develop in all chicks but regress only in those of *P. urinatrix*, possibly with some variation between subspecies in the timing of the regression. Clarification of this point warrants collection of information on further populations of diving petrels.

VOCALISATION

Recordings of the calls of adults of both species in their burrows were made at our request by Dr D. Turner on a Uher 4000 Series recorder at a tape speed of 9.5 cm/s. Copies are lodged with the British

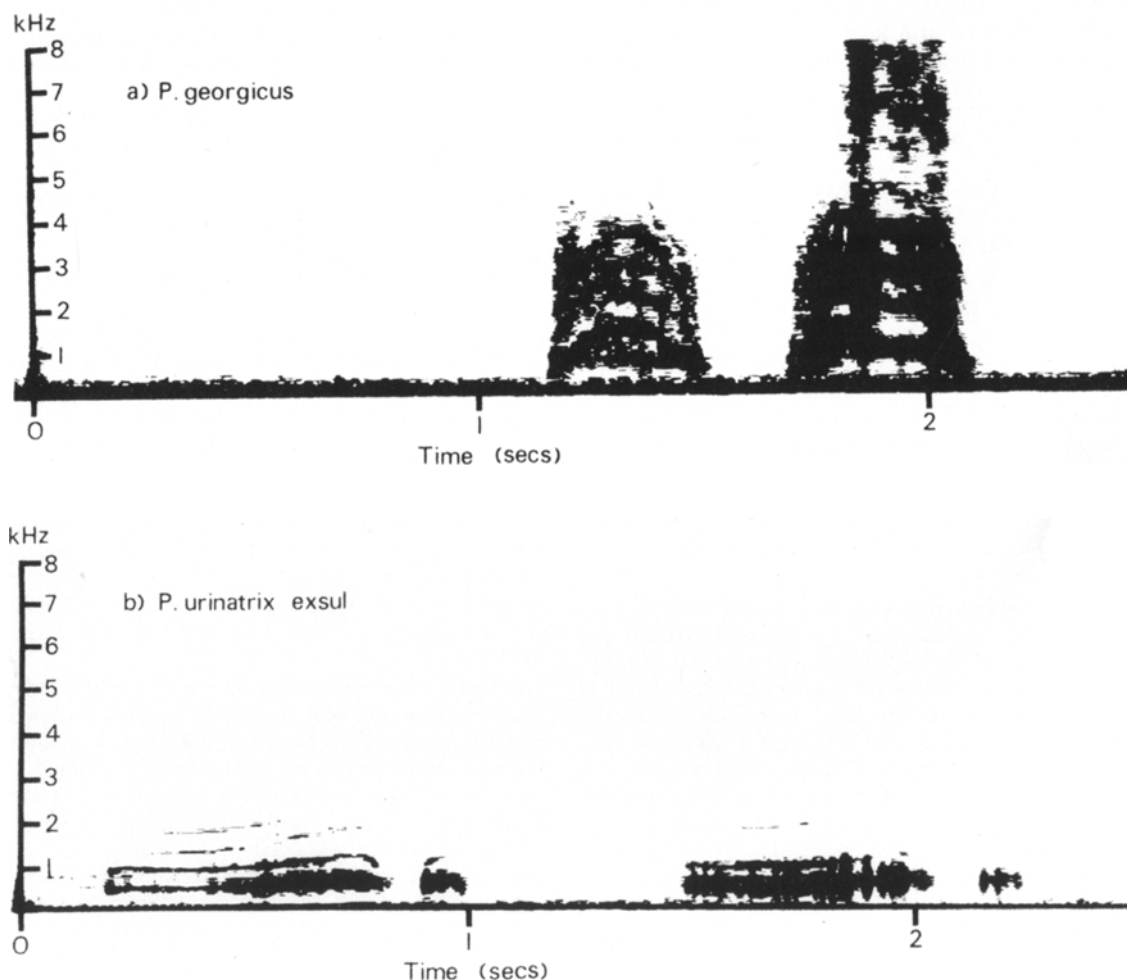


Fig. 4. Sonographs of typical *Pelecanoides* vocalisations: (a) *P. georgicus* – 2 syllables from a long phrase; (b) *P. urinatrix exsul* – 2 complete 2-syllable phrases.

Library of Wildlife Sounds. No attempt was made to establish the range of vocalisation produced, but from experience in the colonies at night the calls recorded were certainly those most commonly heard, and were typical of each species. The social significance of the calls recorded is not known, nor is the status of the birds producing them. In several instances at least two birds seemed to call alternately in the burrow. With *P. georgicus*, recordings of their calls were played back on a cassette tape recorder to stimulate vocalisation. Sonographs were made of some of the recordings of each species; typical results are shown in Fig. 4.

To the human ear, the call of *P. u. exsul* consists of a repeated two-syllable phrase. The first syllable is relatively long, with a rising inflection; the second is short, and lower-pitched than the end of the first syllable. This phrase is uttered about once per second, often for minutes at a time. By contrast, the calls of *P. georgicus* consist of a varying number of similar 'squeaks', usually arranged in phrases of 5–10 syllables of slightly differing duration and separation, followed by a pause of several seconds before the next phrase.

The principal criteria we have found to be of value in separating *P. georgicus* and *P. u. exsul* are summarised in Table 4.

BREEDING BIOLOGY

METHODS

In the initial collection programme about 5 adults were taken from their burrows, together with the contents of the burrow, on 10 occasions spread through the breeding season. Measurements of each bird were taken immediately *post mortem*. The birds were then frozen to await preparation of study skins, sexing, and recovery of food items (5–10 ml of 4% formaldehyde solution was injected into the stomach immediately after death).

The observation programme involved locating nests as early in the season as possible and excavating a separate access tunnel into the nest chamber. The entrance was covered with a rock or a large clump of tussock grass (*Poa flabellata*) when this tunnel was not in use; thus, the birds continued to use the normal tunnel, which was not affected by repeated observations of the nest itself. The disturbance resulting from construction of the extra tunnel preceded—and may have caused—some desertions. Nests were inspected daily when egg-laying or hatching was expected, and the contents were checked by gently pushing a hand beneath the sitting adult, which did not often

seem perturbed. The adult was never actually handled if this could be avoided. After the eggs hatched the nest was not visited for 15 days (or until the guard period was over), to minimise disturbance of adults and reduce the risk of desertion. Subsequently, chicks were weighed daily on a 300 g 'Pesola' spring balance accurate to 1%, and their wing lengths were measured with a 300 mm metal stopped rule. Whenever possible weighings were made at the same time of day (± 1 h). When conditions were very windy weighings were made in the shelter of a wooden box, but accuracy was somewhat reduced. All the *P. u. exsul* chicks and five of the *P. georgicus* chicks were weighed twice daily in 1973–74 to estimate meal sizes.

BREEDING HABITAT

The two species occupy distinct breeding habitats at Bird Island (see Fig. 5). The burrows of *P. georgicus* are found in stony soil with little or no vegetational cover 150–250 m a.s.l. The gradient of the surface may lie anywhere between horizontal and the angle of slip. Damp peat beneath tussock grass on very steep coastal slopes, often above vertical cliffs, contains the burrows of *P. u. exsul*. Such habitat occurs up to 150 m a.s.l. on Bird Island. Although colonies of the two species exist within 50 m of one another, no mixed colonies have been found. Whereas *P. georgicus* colonies are well drained, owing to the nature of the substrate, those of *P. u. exsul* are frequently waterlogged, and may contain standing water. This contributes to the instability of the soil on these steep slopes, and not infrequently earth slips occur in the colonies.

The information available on distribution refers only to Bird Island in any detail, but incidental observations are available from other areas. *P. georgicus* burrows are easy to detect on the open or sparsely vegetated ground in which they occur, but burrows of *P. u. exsul* are more difficult to locate, and are easily confused with those of the larger Antarctic prion, *Pachyptila desolata*.

Colonies of *P. georgicus* occur on most of the suitable areas on Bird Island, where the breeding population probably amounts to thousands. On South Georgia itself colonies are known from a number of sites, up to 3 km inland, and *P. georgicus* is almost certainly a common breeder throughout the island.

Once the preferred habitat could be identified with sufficient precision, it proved possible to locate breeding *P. u. exsul* virtually wherever such habitat occurred on Bird Island. As yet there are no breed-

Fig. 5. (opposite page). Breeding habitat of *Pelecanoides* diving petrels, Bird I., South Georgia: (upper) *P. georgicus*, 150 m a.s.l.; (lower) *P. urinatrix exsul*, 40 m a.s.l.



ing records from South Georgia itself, although fresh corpses have been found at a skua midden, and live birds have been caught at light at two locations (Prince & Payne, in press). It is likely that the species nests at a number of South Georgia sites other than Bird Island, where the population certainly included several hundred pairs at seven known colonies.

PRE-LAYING BEHAVIOUR

The earliest signs of excavation were seen on 27 October 1973, when a number of fresh *P. georgicus* burrows were found on South Georgia island. Over the next 10 days large numbers of freshly dug burrows were completed in this area of fine scree, where no trace of a colony remained from the previous season. The excavation of burrows by *P. georgicus* may have been earlier than normal owing to the early disappearance of snow in this season from the higher ground where they breed. It appears from other observations that this species does not dig through snow, even to occupied burrows. It is probable that during winter and the spring thaw many *P. georgicus* burrows collapse and disappear in the unstable substrate in which they are excavated, as at Heard Island (Downes *et al.* 1959). The same is unlikely to be true of *P. u. exsul*, since the ground would normally still be frozen up to the time when laying can be assumed to commence, in the second half of October. However, their burrows probably survive better than those of *P. georgicus*, since the roots of the dense tussock grass in which they are situated (Murphy & Harper 1921) for *P. magellani*. Thus, in give considerable stability to the soil (Woods 1970).

No direct study of pre-laying behaviour was made, but in the course of daily daytime checks of *P. georgicus* nests to record laying dates some information on nest attendance was gathered. This is presented in Table 5, from which it can be seen that attendance is greatest between 13 and 9 days before laying, and subsequently declines. In the last 5 days before laying we never found more than one bird at a given nest. These birds may have been males, as found by Tickell (1962) for the Antarctic prion. A pre-laying exodus is common in the petrels. It is most marked (and sometimes involves both sexes) in species whose feeding grounds are some distance from the nest (Lack 1966), and is thought to reflect additional feeding effort by the female to form the relatively large eggs characteristic of the Procellariidae, and by the male to lay down fat reserves sufficient to sustain it over the first long incubation shift. Diving petrels are thought to feed close to their breeding areas, so the males at least might not require this feeding interlude. If the above behaviour pattern does underlie the significant decline in daytime nest

attendance ($\chi^2 = 6.886$, $P < 0.025$) before laying, the data in Table 5 suggest that the female's extra effort begins between 15 and 9 days before the egg is laid.

EGG-LAYING, THE EGG, AND INCUBATION

We were able to observe the dates of egg-laying and the duration of incubation only for *P. georgicus*. Laying took place from 7 to 31 December in 1973 ($n = 10$), although in one nest the egg hatched early, and was probably laid on about 19 November. Daily checks of the nests were resumed 40 days after laying, and the mean incubation period of 46 days was determined by direct observation of the 10 nests. This mean excludes an egg that hatched 65 days after laying, outside the range of recorded incubation periods for any population of diving petrels. Since it cannot be confirmed that this egg was continuously incubated (and instances of interrupted incubation were observed), the record has been kept separate from the remaining data. However, it is of interest that the chick hatched and subsequently fledged normally.

By reference to Thoresen's (1969) determination of 54 days for the incubation period of *P. u. urinatrix* it appears from the *P. u. exsul* hatching dates (see Table 8) that laying takes place from 20 October until 7 November.

The weights and dimensions of eggs from Bird Island are shown in Table 6, in comparison with those of *P. urinatrix* subspp. eggs from the New Zealand studies. The figures show very little difference between *P. u. urinatrix*, *P. u. chathamensis*, and *P. georgicus*, although *P. u. chathamensis* eggs may be slightly smaller. However, *P. u. exsul* eggs are considerably larger, especially along the long axis. This reflects the more pointed nature of the *P. u. exsul* egg, clearly apparent when it is seen beside the egg of *P. georgicus* (Fig. 6).

The weight data must be treated with caution. Tickell (1968) found that wandering albatross (*Diomedea exulans*) eggs lost about 15% of their new-laid weight during incubation, and a linear regression of the weights of *P. georgicus* eggs against time suggests that a similar value holds good for this species. Our recorded weights of *P. u. exsul* eggs are all from the latter half of incubation, as are Thoresen's data. Richdale's figures refer mainly to deserted and addled eggs, and cannot be compared at all. Only *P. georgicus* eggs were weighed at all stages of incubation, and so may be slightly 'heavy' in relative terms. This bias is not likely to be large enough to influence the trend in Table 7, which expresses egg weights as a percentage of the body weight of breeding adults, and suggests that eggs are relatively larger at higher latitudes.

Table 5. Nest attendance by *Pelecanoides georgicus* adults before egg-laying. South Georgia (all observations up to 12 days before laying were made at the same nest).

[illegible]

Table 6. Weights and dimensions of eggs of *Pelecanoides georgicus* and *P. urinatrix* subsp.

Mean	S.D.	Range	n	Source
	WEIGHT (g)			
<i>P. u. urinatrix</i>	16.61	14.5-20.0	14	Thoresen (1969) (late-hatch- ing eggs); North I. N.Z.
<i>P. u. chathamensis</i>	14.9	11.0-18.25	27	Richdale (1965) (most desert- ed); Stewart I., N.Z.
<i>P. u. exsul</i>	18.84	15.5-21.5	31	This study
<i>P. P. georgicus</i>	17.39	13.1-20.5	29	This study
	LENGTH (mm)			
<i>P. u. urinatrix</i>	37.86	35.9-41.8	15	Thoresen (1969)
<i>P. u. chathamensis</i>	37.7	34.5-42.0	39	Richdale (1965)
<i>P. u. exsul</i>	40.18	37.0-44.0	37	This study
<i>P. P. georgicus</i>	37.68	34.5-41.3	32	This study
<i>P. P. georgicus</i>	37.9	34.6-41.3	8	Despin <i>et al.</i> (1972); Crozet I.
<i>P. P. georgicus</i>	38.6	36.0-41.0	no data	Paulian (1953); Kerguelen I.
	WIDTH (mm)			
<i>P. u. urinatrix</i>	30.56	28.0-30.7	15	Thoresen (1969)
<i>P. u. chathamensis</i>	29.4	27.25-31.5	39	Richdale (1965)
<i>P. u. exsul</i>	31.62	29.5-33.2	37	This study
<i>P. P. georgicus</i>	30.55	29.0-32.0	32	This study
<i>P. P. georgicus</i>	31.2	29.0-33.4	8	Despin <i>et al.</i> (1972)
<i>P. P. georgicus</i>	32.5	30.5-33.2	no data	Paulian (1953)

Table 7. Egg weight of *Pelecyanoides* diving petrels as a percentage of adult weight (measured during chick feeding for all populations); sources as in Table 6.

	Egg weight (g)	Adult weight (g)	%
<i>P. u. urinatrix</i>	16.61	136	12.2
<i>P. u. chathamensis</i>	16.61*	124	13.4
<i>P. u. exsul</i>	18.84	128	14.7
<i>P. georgicus</i>	17.39	103	16.9

*By comparison with *P. u. urinatrix* egg weight, probably an overestimate of the true value.

Table 8. Timing and duration of events in the life cycle of *Pelecoides urinatrix exsul* and *P. georgicus* at Bird I., South Georgia, 1973-74 and 1974-75: mean \pm standard deviation, range (in parentheses), and sample size (in italics).

	<i>P. u. exsul</i>	<i>P. georgicus</i>
Egg laying	No data	12.1 Dec \pm 7.00 (7-31 Dec) 10
Hatching	18.4 Dec \pm 4.47 (14-31 Dec) 18	28.5 Jan \pm 10.85 (4-30 Jan) 20
Fledging	9.4 Feb \pm 3.44 (4-14 Feb) 16	14.3 Mar \pm 10.22 (4 Mar-2 Apr) 18
Incubation	No data	46.35 \pm 1.56 (44-49) 10
Fledging	(50-58) 16 53.9 \pm 2.56	45.5 \pm 1.47 (43-48) 18

HATCHING AND FLEDGING

These aspects were fully covered for both species. Because nests were not visited for 15 days after hatching, nothing is known of the attendance of the adult over this period. However, the chicks were always alone by day from the time daily checks were recommenced until the chicks left the burrows.

The results (Table 8) show that *P. u. exsul* hatched some 41 days earlier than *P. georgicus* in 1973–74, and that fledging took about 8 days longer in *P. u. exsul*. Estimates of the age of chicks collected in the 1972–73 and 1973–74 seasons—calculated from mean growth curves, and taking 1973–74 as a baseline—indicate that both species bred about 10 days earlier in 1971–72 (*P. u. exsul* data not obtained in this season). There seems to be little difference between 1973–74 and 1975–76 for *P. u. exsul*, and for both species 1973–74 seems to have been a typical season. The winter of 1972 was unusual in that deep snow and ice persisted rather longer than usual both on the ground and in burrows, and this may explain the lateness of breeding by both species in the following summer. Richdale (1965) reported variation from season to season in the timing of breeding by *P. u. chathamensis*, unlike some other Procellariiformes.

CHICK GROWTH

Wing length data for chicks of both species (Fig. 7) show that wing growth is much more rapid in *P. georgicus*; its wing is 50% longer than that of *P. u. exsul* at age 20 days. The two New Zealand studies show results very similar to the *P. u. exsul* curve (Fig. 7).

Weight data (Fig. 8) are presented as percentages of adult weight, for ease of comparison. It is apparent that *P. georgicus* chicks gain weight faster, peak earlier and at a higher weight (141% of mean adult weight, cf. 122 for *P. u. exsul*), and then lose weight more rapidly to fledge earlier at adult weight. As a result of variation in age at fledging between individual chicks, a better impression of weight change towards this time is gained by plotting days before fledging against weight (Fig. 9). There is a clear difference between *P. georgicus*, *P. u. exsul*, and the other population for which data are available, *P. u. chathamensis*.

It is possible that daily measurement caused sufficient disturbance to the chicks to influence their growth; even in an undisturbed population a proportion of chicks may have poor growth rates, for a number of reasons. Rather than subjectively eliminate possible runts from the data, we have presented the results for all chicks that appeared to fledge successfully. Calculating mean values, while showing the trend for each species, will underestimate the realistic weight curve, so the weight curve of the heaviest (most successful?) individual of each species is shown (Fig. 10) for comparison. These curves are very substantially higher. Another noticeable character is that the *P. u. exsul* curve is rather irregular, suggesting erratic feeding. This is borne out by analysis of the daily weight changes.

FEEDING THE CHICKS

Information on meal size and frequency was obtained by weighing five *P. georgicus* chicks twice

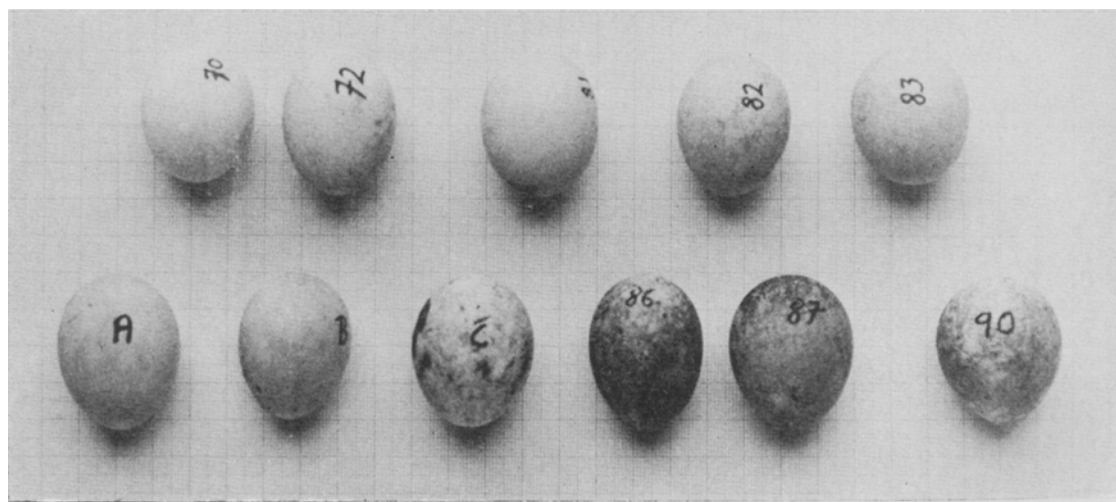


Fig. 6. Eggs of *Pelecanoides* diving petrels, South Georgia: top row, *P. georgicus*; bottom row, *P. urinatrix exsul*.

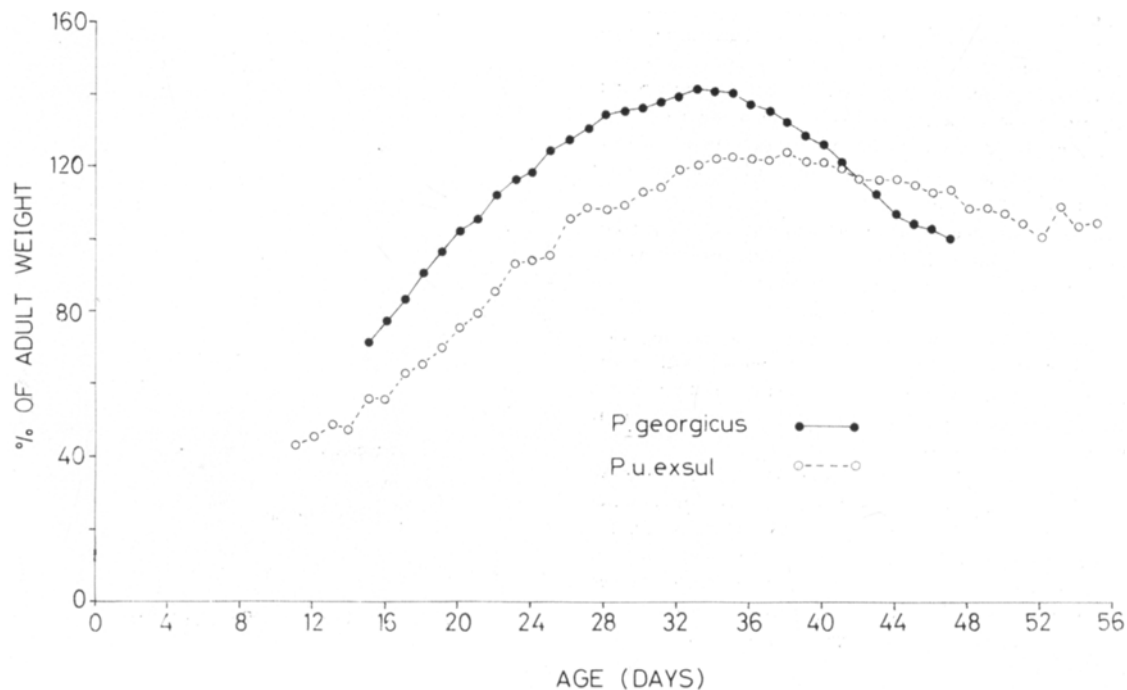


Fig. 7. Growth of the wing in chicks of *Pelecanoides georgicus* ($n = 18$, this study), *P. urinatrix exsul* ($n = 11$, this study), *P. u. urinatrix* ($n = 14$, Thoresen 1969), and *P. u. chathamensis* ($n = 2-30$, Richdale 1943).

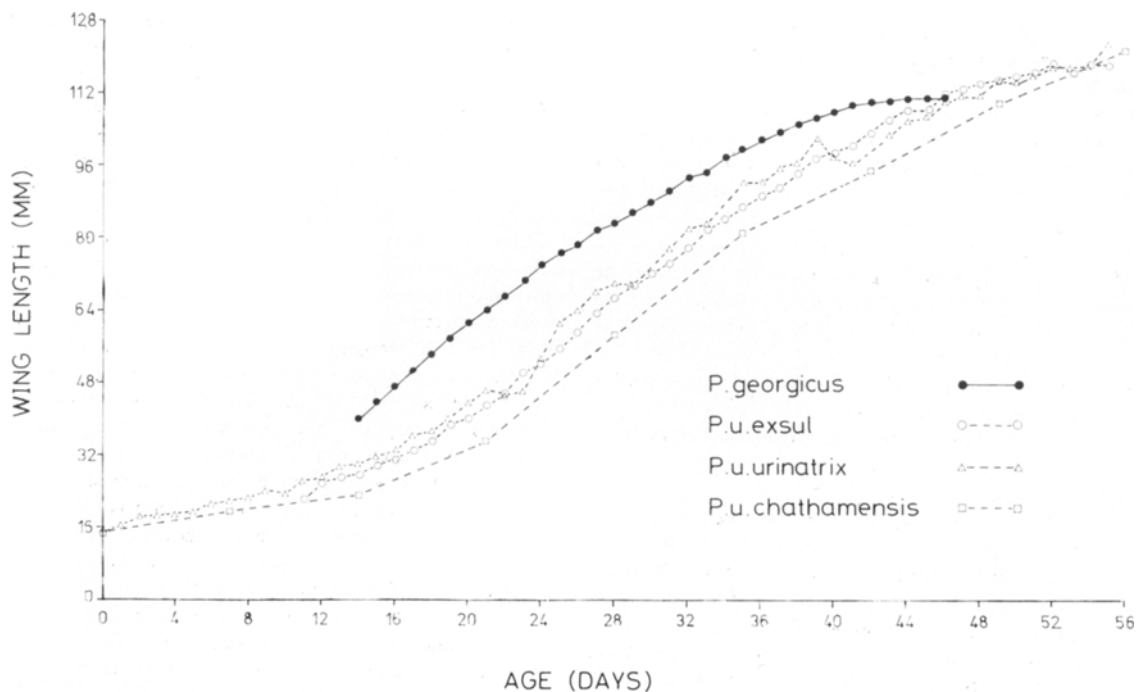


Fig. 8. Growth in weight of chicks of *Pelecanoides georgicus* ($n = 18$) and *P. urinatrix exsul* ($n = 11$), Bird I., South Georgia; *P. georgicus* data collected 1973-74, *P. u. exsul* 1975-76. Adult weights (mean) - *P. georgicus* 103.2 g. *P. u. exsul* 128.6 g.

daily from age 15 days until fledging. The same procedure was carried out with the 1973-74 *P. u. exsul* chicks, but their growth was so erratic that the results obtained may not be typical, and must be treated with caution. The evening weights of *P. georgicus* chicks handled twice daily do not differ greatly from the mean for the total sample of this species.

On average, *P. u. exsul* chicks lost weight in 26.7% of 105 evening-to-evening 24 h periods between the ages of 15 and 25 days, whereas *P. georgicus* chicks lost weight in only 10.2% of 176 such periods. Conversely, in the same number of observations *P. u. exsul* chicks had gained more than 14.9 g in 16.2% of instances, as against 3.4% for *P. georgicus*. If chicks of the two species are of similar physiology and behaviour, then those of *P. u. exsul* are probably fed larger quantities less regularly.

The *P. georgicus* chicks were weighed within 30 min of 0930 h and 1930 h Greenwich Mean Time. Adults generally began to arrive at about 2330 h, so morning weighings were some 10 h after the beginning of feeding. Loss of weight during these hours is potentially a major source of error in estimating meal size. Harper (1976) demonstrated for the similar-sized fairy prion, *Pachyptila turtur*, that about 50% of the weight of a meal was lost within 14 h of the start of feeding. We investigated this point by weighing 11 *P. georgicus* chicks at 3-h intervals over a 24-h period. It was not possible to determine when meals were fed (cf. Harper's study), and the weighings revealed only overall weight changes, incorporating metabolic losses. It is likely that some weighings interrupted or even prematurely curtailed feeding. Thus, the weight increases recorded will underestimate true meal size.

Some chicks were fed in more than one 3-h period; in these instances the second weight change would underestimate the weight of food received by even more, owing to the presumably increased rate of weight loss consequent on the initial feeding. This was observed to be 10-15 g per 3-h period with some chicks. In spite of these tendencies to underestimate the food received, the data obtained are of some value, and are shown in Table 9.

Two chicks (I and J, Table 9) did not receive substantial feeds, and have been ignored for calculation purposes. The remaining chicks received an average recorded value of 37.1 g of food each, but by morning the conventional estimate of meal size showed mean increases of only 20.3 g. Thus, at least 45.3% by weight of the food received had already been lost by the nine chicks at ages 9-39 (mean 23.4) days.

No account is taken of the increased digestive capacity of older chicks. The existence of such an increase from a newly hatched chick of 13 g to a

fully fledged one of 100+ g is intuitively apparent. However, the comprehensive data on actual meal size and weight changes at different ages necessary to evaluate this were not obtained in our study. Thus, although the data on apparent meal size collected by morning weighings are useful for comparative purposes, they cannot be used for absolute determinations.

Apparent meal size, plotted against age in Fig. 10, shows a marked decline as the chick grows, and this may be entirely an artefact reflecting the increased digestive capacity of the chicks. Information from the 3-h weighings (Table 9) suggests certain minimum values for meal size. Assuming only a single visit per night by each adult, the 56 g increase of chick F implies that adults can carry at least 28 g of food each. Fig. 11 shows that the apparent meal size of 28 g revealed by the morning weighing of chick F after its 56-g meal is consistent with other maximum apparent meal sizes for chicks of similar ages. Chick H, at about 32 days old, received at least 43 g of food but still lost weight. Chick E at about 25 days old, received at least 39 g of food and was able to maintain its weight. Chicks of these ages are normally still gaining weight, so normal

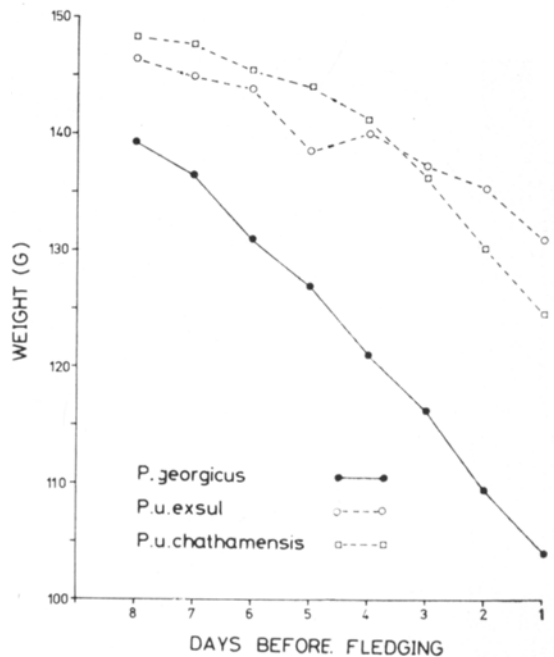


Fig. 9. Weight loss before fledging of chicks of *Pelecanoides georgicus* (1973-74, $n = 18$, this study), *P. urinatrix exsul* (1975-76, $n = 11$, this study), and *P. u. chathamensis* ($n = 46$, Richards 1943).

meals probably exceed about 40 g for older chicks, with a maximum in the region of 60 g. These figures are comparable with Harper's finding that fairy prion adults each bring 21.1–30.1 g of food to the chick nightly.

Use of the meal size data to estimate feeding frequency depends on knowledge of the amount of weight lost by a chick that remains unfed, which must vary with age. In only one instance could a chick positively be said to have been unfed for a night, and this 16-day-old bird lost 9 g in 24 h. Weight losses of this magnitude or greater by chicks that had not yet attained peak weights occurred on only four occasions (three involving the same individual) in 309 bird/nights (1.3%). The 9 g weight loss is probably not an accurate criterion of feeding as regards larger chicks, which decline in weight even when fed. Thus, chicks are probably fed on more than 98% of possible nights.

It is not possible to ascribe variation in apparent meal size to attendance by one or both parents, but

the high frequency of attendance imputed above suggests that both parents are often present, since a high proportion of apparent feed sizes in the first few days of weighing exceed 20 g. There is no evidence to suggest that adults bring more than one load of food each in a night, nor has this been reported in other detailed studies. However, it is clear from Table 9 that feeding may take place at any time of night. For instance, chicks B and D reached peak weight at 0600 h, and so must have been fed substantial amounts after 0300 h. Both chicks had received a meal earlier, and both were comparatively young (less than half the mean age at fledging). These latter meals may therefore have 'topped up' the crop content of chicks unable to accept all the available food earlier in the night.

Comparable data for *P. u. exsul* are limited. It can be assumed that adults can carry similar or greater quantities of food, since apparent meal sizes in excess of 30 g and even occasionally 40 g were observed. Weight losses of 9+ g over a 24 h period

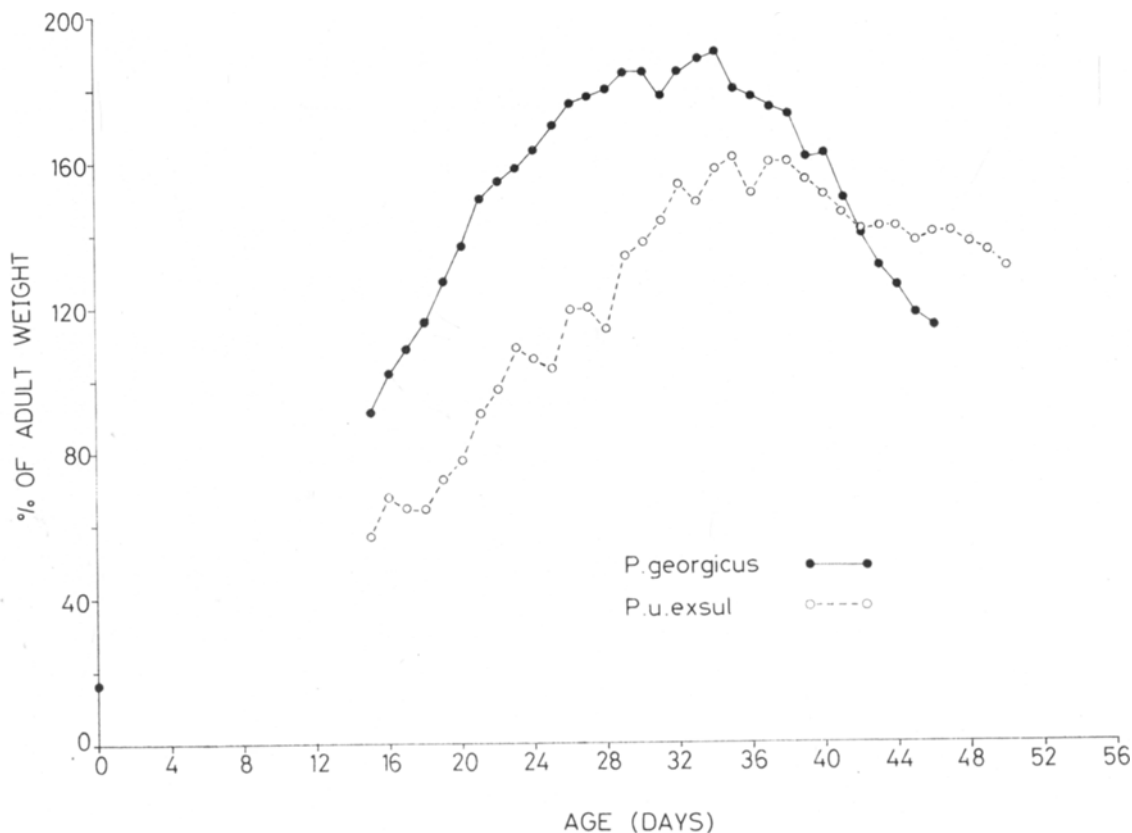


Fig. 10. Growth in weight of heaviest individual chick of *Pelecanoides georgicus* (1973–74) and *P. urinatrix exsul* (1975–76), Bird I., South Georgia. Adult weight as in Fig. 8.

in chicks still approaching peak weight numbered 12 out of 271 bird/nights (4.4%), suggesting that chicks are visited on more than 95% of possible nights.

FOOD

Organisms fed to the chicks were identified by examining the stomach contents of chicks taken as speci-

mens. Digestion usually prevented the identification to species of much of the food material, but it was still possible to ascribe most food items to subclass or suborder. Species positively identified were: Copepoda – *Calanoides acutus*, *Rhincalanus gigas*; Amphipoda – *Hyperoche medusarum*, *Hyperietta antarctica*, *Parathemisto guadichaudii*, *Cylopus lucasii*; and Euphausiacea – *Euphausia superba*. All occurred in

Table 9. *Pelecanoides georgicus* chicks weighed at 3 h intervals over a 24 h period, South Georgia, 22–23 Feb 1974. Age estimated from wing length data in Fig. 6. 'a' indicates presence of adult; peak weights in bold type. 'Minimum food', sum of weight gains between 2130 h and 0600 h; 'apparent food', 0900 h weight minus previous 2130 h weight.

Chick	Age (days)	Weight (g) at time (h GMT)									Minimum food (g)	Apparent food (g)	24-h change (g)
		2130	2400	0300	0500	0900	1200	1500	1800	2130			
A	9	62	80a	96a	90	86	80	74	71	69	34	24	+7
B	9	56	57	82a	90	85	80	73	70	66	34	29	+10
C	21	103	117a	134a	125	119	112	107	105	104	31	16	+1
D	21	111	130a	125a	139	137	126	120	116	115	33	26	+4
E	25	145	145	184	170	162	159	153	148	145	39	17	0
F	27	130	186a	176a	166	158	149	144	137	136	56	28	+6
G	28	148	154a	183	178	168	162	153	149	150	35	20	+2
H	32	158	201a	186a	179	171	166	161	159	155	43	13	-3
I	34	142	143	139	136	135	135	134	131	130	1	-7	-12
J	37	161	157	155a	159	159	152	151	152	147	4	-6	-14
K	39	160	189a	180	175	170	165	158	160	155	29	10	-5
Mean:	23.4										37.1	20.3	+2.4

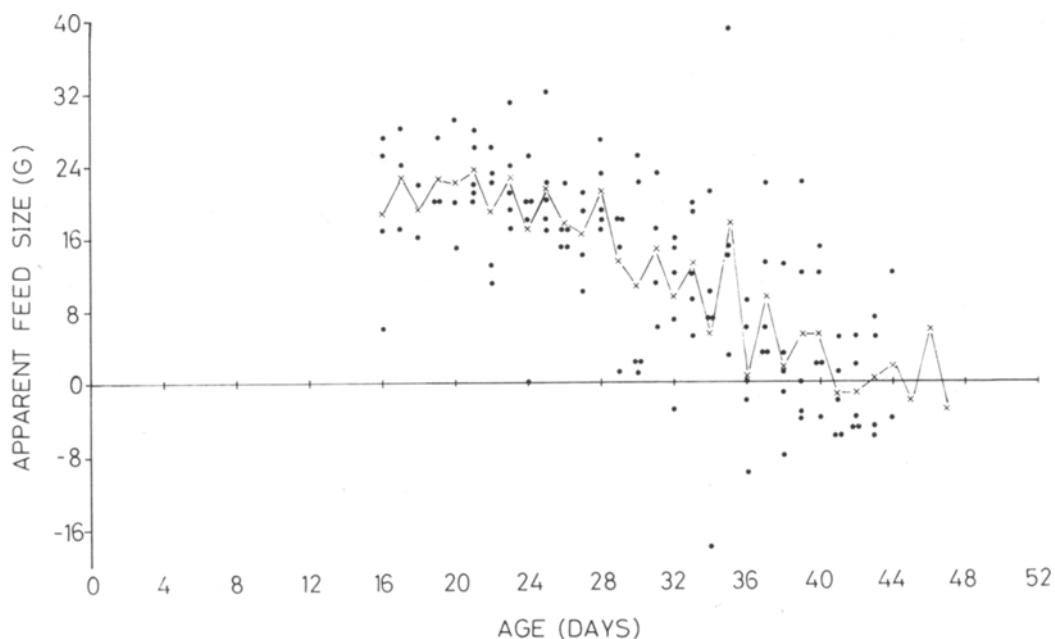


Fig. 11. Apparent meal size (difference between morning weight and previous evening weight) for 5 *Pelecanoides georgicus* chicks, Bird I., South Georgia, 1973–74 (×—×, change in mean apparent feed size). See text for further explanation.

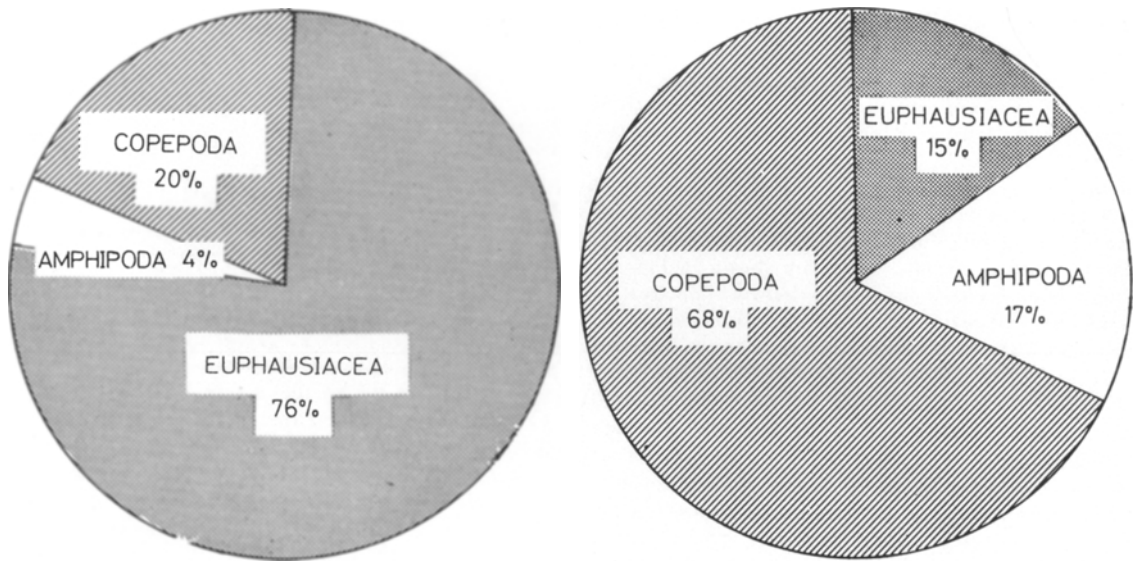


Fig. 12. Approximate composition by volume of food from stomachs of (left) 17 *Pelecanoides georgicus* and (right) 15 *P. urinatrix exsul* chicks, Bird I., South Georgia. Data obtained in 1971-72 (1 *P. georgicus* sample), 1972-73 (16 *P. georgicus* and 4 *P. u. exsul* samples), and 1973-74 (remaining *P. u. exsul* samples)

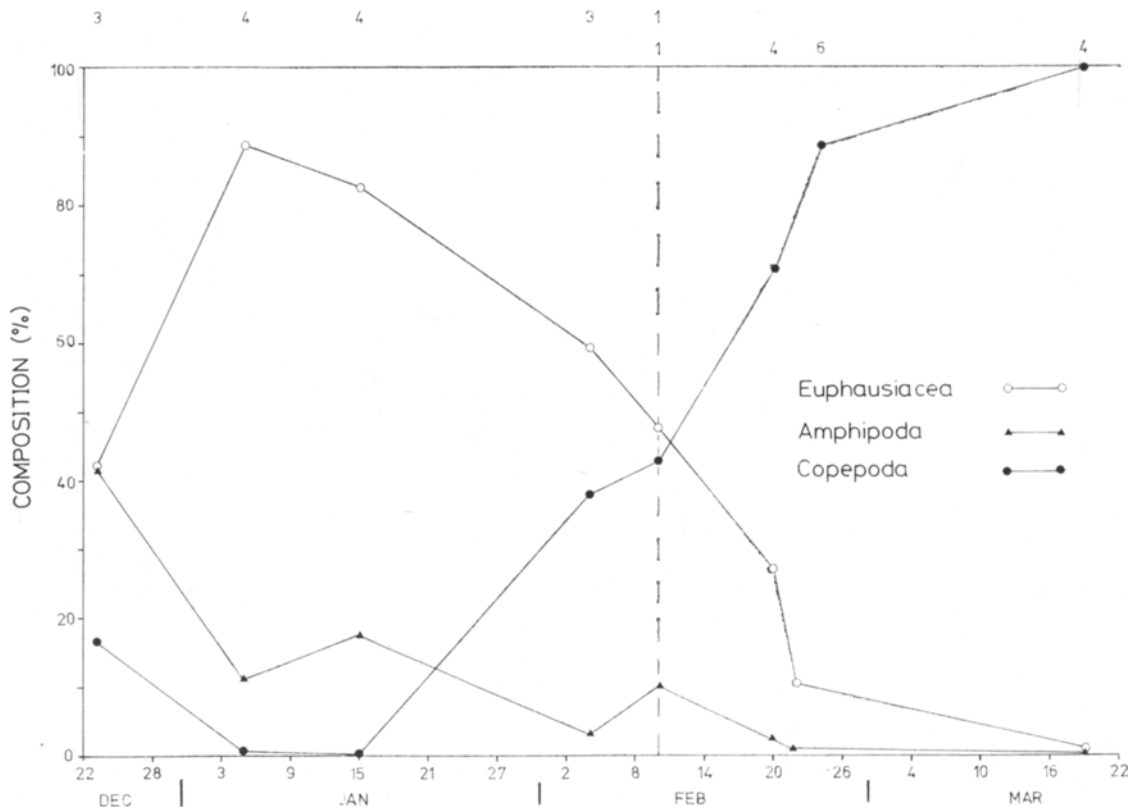


Fig. 13. Seasonal change in composition of diet of 30 diving petrel chicks, Bird I., South Georgia. All samples before and 1 on 10 Feb are from *Pelecanoides urinatrix exsul*, remainder from *P. georgicus*.

the food of both species, except that *C. lucasii* was found in one *P. georgicus* sample only. Identification to species of some food items was possible in most of the *P. u. exsul* samples, but in very few from *P. georgicus*. Most *E. superba* were post-larvae (10–13 mm), with only the occasional adolescent (30–40 mm).

Visual estimates were made of the proportion of each food sample contributed by the major groups, and the means of these values are shown in Fig. 12. There are marked differences between species in proportions of prey items fed to the chicks; copepods dominate the *P. u. exsul* samples, whereas euphausiids are more abundant in *P. georgicus* material. However, if the composition of the food material is examined by date, it can be seen that in both species there is a trend from a predominance of copepods in early summer to a very high proportion of euphausiids later in the season. By combining the data it is possible to gain a picture over a longer period. It is not simply the availability of prey species or groups that is involved, since in late summer, when copepods are disappearing from the diet of the diving petrels, they are still an important food item for Antarctic prions (Prince, in press). In the context of the seasonal trend suggested in Fig. 13 it is difficult to comment on possible prey selection by two species rearing their chicks at different times. Also, without information on the feeding mechanism of diving petrels it is not clear how the results obtained relate to the relative abundance of prey species.

MOULT

A number of *P. u. exsul* adults had begun to moult the primaries before their chicks fledged. On 4 February 1973 one out of six birds had shed a primary, and 6 days later each of four adults examined had lost up to four primaries from each wing and one had a fully grown new feather. Falla (1937) reported that moulting was well advanced in this species at Kerguelen during February, and complete in one individual on 23 February. He made no mention of synchronous moulting, as reported by Murphy & Harper (1921) and Watson (1968) for *P. garnoti*, and it seems that at South Georgia and Kerguelen *P. u. exsul* shows normal sequential moulting. We have records of a further four moulting birds from South Georgia examined on 10–12 February 1976 in which up to half the primaries had been shed in the normal proximal-distal sequence. There is a literature record of two *P. urinatrix* (subspecies not cited) that were in synchronous moult picked up dead on New Zealand beaches (Watson 1968).

We observed no moulting specimens of *P. georgicus* among the large numbers we handled between De-

cember and March, which included adults at a comparable stage in their breeding cycle to the moulting *P. u. exsul* examined.

PREDATORS

Diving petrel remains are often found at the abundant skua middens on South Georgia, but rarely in any numbers. The predatory habits of skuas are probably the major reason for the petrels' nocturnal habits, and it is noticeable that activity in a colony is much reduced when there is bright moonlight, which might enable the skuas to operate efficiently. Chicks of both *P. georgicus* and *P. u. exsul* are sometimes dug out of shallow burrows, and skuas have been seen to be the culprit on a number of occasions. It is probable that any chick which draws attention to itself by calling when at or near the surface is liable to be killed. Skuas breed near most *P. u. exsul* and some *P. georgicus* colonies, and 'off-duty' birds are frequently at *P. georgicus* colonies outside defended territories.

Little is known of other predators. There is one record of a *P. u. exsul* head in a food sample regurgitated at the nest by a giant petrel, *Macronectes halli*, on Bird Island (J. W. H. Conroy, pers. comm.). There is also a record of a leopard seal, *Hydrurga leptonyx*, stomach containing 3 diving petrels among 12 small petrels (Paulian 1953). Leopard seals are common around South Georgia, especially in winter, when diving petrels are among the few species still present in any number.

PARASITES

All 54 *P. u. exsul* and 50 *P. georgicus* specimens were carefully examined for ectoparasites in the plumage. Feather lice (Mallophaga) were found on 39 (72%) *P. u. exsul* and 44 (88%) *P. georgicus*. All the infested *P. u. exsul* carried *Pelmatocera setosa* (Giebel, 1876) and two also carried *Austromenopon elliotti* (Timmerman, 1954). All but one infested *P. georgicus* carried *Pelmatocera enderleini* Eichler, 1949; the exception carried *A. elliotti* alone. Two *P. georgicus* carried both species of louse. It appears from this series and from most published data (Clay & Moreby 1970) that the two species of *Pelmatocera* considered here are host specific, but one literature record appears to contradict this—at Kerguelen, Paulian (1953) found *P. setosa* infesting both diving petrels. In view of the short time since *P. enderleini* was described when Paulian's work was carried out, the possibility of an oversight in louse identification must be borne in mind.

One *P. u. exsul* was carrying a number of examples of the free-living mite *Androlaelaps pachyptilae* (Zumpt & Till, 1965), which has been recorded from bird nests on South Georgia and Heard Island (Hunter 1970).

Gut parasites have been examined from only 12 *P. georgicus* and 5 *P. u. exsul*. One tapeworm, *Tetrabothrius* sp., and one nematode, *Stegophorus heardi* Mawson, 1953 were found in both species. *Tetrabothrius* was represented by a single immature example in each species, and our record of the genus as a parasite of *P. georgicus* is apparently new; Williams *et al.* (1974) have recorded it in *P. u. exsul*.

DISCUSSION

Difference in the breeding habits of *P. georgicus* and *P. u. exsul* has been found at Heard Island and Marion Island (Rand 1954, Downes *et al.* 1959) as well as South Georgia. The altitudinal difference observed at both Marion and Bird Islands probably reflects climatic influences on the distribution of their respective habitats. At both Heard Island (Downes *et al.* 1959) and South Georgia (Murphy & Harper 1921) *P. georgicus* is reported to breed down to sea level.

P. georgicus has often been found nesting on level ground, where it runs several metres before becoming airborne, even in a moderate wind. Such a run is impossible in the heavily vegetated areas inhabited by the morphologically similar *P. u. exsul*. This may account for the latter's choice of steep breeding sites, sometimes above cliffs, where take-off would be facilitated.

The 40-day difference in hatching dates between the two species at Bird Island appears to be related to the time of clearing of the winter snow and ice accumulations in and around the burrows. The steep, low-lying sites used by *P. u. exsul* accumulate less snow and clear earlier in the spring than those used by *P. georgicus*. The variation in mean breeding data from season to season, together with the late breeding of both species following the relatively severe winter of 1972, tend to support this view.

The eggs of the two species are fairly similar in size but, relative to adult weights, that of *P. georgicus* is proportionately rather larger. In diving petrel populations for which adequate egg-weight data exist (see Table 7), the egg becomes proportionately larger with increasing latitude.

The breeding cycle parameters established for *P. u. exsul* (fledging period and chick growth curve) are similar to those determined for the other two *P. urinatrix* subspecies so far studied (Richdale 1965, Thoresen 1969), from which it may be supposed that the incubation period differs little from Richdale's estimate of about 8 weeks or Thoresen's 53.5 days \pm 4 h. In contrast, the data obtained for *P. georgicus* are strikingly dissimilar from the only other figures published (Despin *et al.* 1972). These refer to the Crozet Islands, where fledging periods of 53 and 54 days were recorded for chicks with growth

curves indistinguishable from those we obtained for *P. u. exsul* at South Georgia. Furthermore, Despin *et al.* cite without reference an incubation period of 55 days not obtained by themselves, but which has appeared in subsequent literature (Watson 1975). Since the figures from the Crozet work are at variance with our results, and in view of the small sample size ($n = 2$) and the failure of a large proportion (seven out of nine) of the nests observed, it seems likely that they may be atypical, and do not constitute a demonstration of differences between *P. georgicus* populations. It is possible that they are based on a misidentification.

Our data for *P. georgicus* demonstrate that both fledging and incubation are completed more quickly than in any other diving petrel species or subspecies so far studied, and give rise to a characteristic growth curve (see Fig. 6 & 7). At South Georgia fledging takes 8.4 days less than with *P. u. exsul*, and a similar shortening of the incubation period would contract the breeding period by 16–17 days overall.

The mechanism underlying this contraction is not clear. It may involve higher metabolic activity from the earliest stages of chick development. The growth curve differences, with the size and frequency data on chick meals, suggest more assiduous feeding by *P. georgicus* adults combined with an earlier ability of the chick to accept the full food burden the adults can deliver. With this in mind, one could envisage the thicker primary down of the *P. georgicus* chick enabling it to thermoregulate successfully at an earlier age, thus releasing the adult for foraging. The thicker down could equally well represent another adaptation by *P. georgicus* to the rigours of its environment, whereas *P. u. exsul* appears to be little different from the other subspecies of *P. urinatrix* in breeding adaptations.

Examination of their breeding ecology has shown that, within the confines of their very similar morphology, *P. u. exsul* and *P. georgicus* are distinct in many ways. *P. u. exsul* uses breeding sites with a less extreme microclimate that are habitable early in summer. Consequently, breeding begins earlier and can be extended over a longer period. The egg is proportionately small, and produces a small chick whose slower subsequent development may be related to a less rigorously maintained feeding regime. *P. georgicus* breeds in habitat that cannot be occupied until mid season. Its shorter breeding cycle is the logical counter to this, and its relatively larger egg is consistent with more rapid early development of the chick. These differences in breeding strategy appear sufficient to permit the two species to co-exist at South Georgia; similar differences presumably occur at the other islands where both species breed.

The present distribution and morphological charac-

ers (including the black line on the tarsus) of *Pelecanoides* spp. suggest it is possible that an original diving petrel stock may have been split into two main groups during a glaciation that isolated the South American and New Zealand populations from each other. These then evolved in isolation, and it is likely that their southernmost representatives (*P. georgicus* and *P. u. exsul*) have come together relatively recently. It is likely that allopatrically evolved differences became accentuated in sympatry, and the present situation of distinct breeding habitat and season evolved. The importance of other biological differences—particularly those operating away from the breeding site and outside the breeding season—are not conclusive. *P. u. exsul* does begin to moult while still feeding chicks, a feature not seen in *P. georgicus*. Furthermore, the data show that *P. u. exsul* moults its flight feathers sequentially, whereas some of the *P. georgicus* group of species moult synchronously. These differences may be correlated with a more pelagic and migratory winter distribution of *P. u. exsul* and a more inshore winter distribution of *P. georgicus*.

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