ADULT SURVIVAL ESTIMATES FOR TWO ANTARCTIC PETRELS

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ABSTRACT. This paper gives estimates of the mean annual adult survival rates of the cape pigeon (*Daption capensis*) and the snow petrel (*Pagodroma nivea*), based on banding data from Signy Island, South Orkney Islands. These data are imperfect in that there has been incomplete recapturing of the marked populations in most years, and also much band loss. The cape pigeon has a mean adult survival of approximately 94–95 per cent per annum, equivalent to a mean reproductive life span of between 16 and 20 yr.; this petrel will begin breeding in its fourth year of life, and on theoretical grounds it is believed that its pre-breeding mortality (between fledging and maturity) is of the order of 65–70 per cent. Less accurate data are available for the snow petrel; the mean adult survival rate is between 93 and 96 per cent per annum, indicating between 14 and 24 yr. of adult life; the length of its pre-breeding period is not known. Finally, comparisons are made between the above figures and survival data for others of the Procellaridae.

THE bird-banding scheme of the British Antarctic Survey has been in existence since 1945, and progress reports have been given by Sladen and Tickell (1958) and Hudson (1963). In recent years large-scale banding has been confined to Signy Island (lat. 60°43′S., long. 45°36′W.) in the South Orkney Islands, where work started in 1948. The present analyses were made exclusively with Signy Island data.

Nearly all banding (and subsequent recapturing of banded birds) has been done by amateur ornithologists as and when their other duties permitted. This, together with the fact that enthusiasm for the banding programme has been less in some years than in others, has inevitably introduced bias; nevertheless, the body of data accumulated since 1948 is substantial. The present paper was undertaken to assess the usefulness of the British Antarctic Survey banding data for survival studies.

In this paper, an estimate has been made of the mean annual adult survival rates (and thus life estimates) for two petrels which breed in substantial numbers in the South American quadrant of Antarctica; these are the cape pigeon and the snow petrel. On Signy Island, both species were marked for the first time in March 1948, though not in any quantity until 1952. Most have been banded as adults at the nest, and by recapturing them in subsequent years it has been possible to follow many over long periods; it is these records, based on breeding adults, that have been used here. Large numbers of nestling cape pigeons have been banded, but few snow petrels; as yet there are too few recoveries of either for the survival/mortality rates of immature birds to be calculated. It must be remembered that both these species, in common with most (if not all) of the larger Procellaridae, are likely to have lengthy periods of immaturity.

METHODS

At British Antarctic Survey stations, ornithological work has (with a few notable exceptions) been occupational therapy, with great disparity of effort between years according to the interests of the men who were present. This applies as much to Signy Island as elsewhere. For no two consecutive years has the effort put into recapturing marked birds been complete enough for a direct comparison between them, and so it has not been possible to consider the survival from one year to the next. The alternative approach has been used of considering what proportions of the marked populations survived for x yr. (i.e. for 4, 8, 12, etc. yr.) after banding. This approach is concerned with proportions in age groups, and the resulting survival estimates do not relate to any particular years.

For this type of analysis it is necessary to assume that all individuals at risk have the same probability of dying over any time interval. Lack (1954), in a review of mortality studies, considered that the probability of survival is independent of age once adulthood is achieved. However, the possibility of senility occurring in wild populations, especially of potentially long-lived birds, has not been tested adequately. Austin and Austin (1956) have shown that this probably occurs in the common tern (*Sterna hirundo*), while senility has been claimed for

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one Eurasian passerine—the pied flycatcher (*Ficedula hypoleuca*) (Berndt and Sternberg, 1963). The very large marked samples necessary to test for senility are not available for the present study.

Three types of bias are likely to be present in the British Antarctic Survey banding/recapture data:

i. Since disappearance from the record is equivalent to death, emigration from the study population would result in some degree of underestimation. Both the cape pigeon and snow petrel are known to be tenacious of their particular nesting sites, and since only data on established breeders have been used, this aspect is unlikely to be important.

ii. More serious is the certainty that the metal bands will not last for the full life span of such long-lived birds as these petrels, and loss of band equals disappearance from the record. Until monel metal was introduced in 1960, the bands used on Signy Island were of soft-temper aluminium alloy. Re-banding at intervals has been necessary in order to follow the older individuals over long periods; in all, 78 per cent of the cape pigeons and 52 per cent of the snow petrels on which this paper is based have been re-banded, some of them thrice. It is suspected that many birds (particularly those banded before 1955) have been lost from the record because they had lost their bands, and this is perhaps one reason why so few banded as nestlings have been recaptured at breeding age. Many of the aluminium bands showed wear within 4 yr. and could be expected to fail at 5 or 6 yr.; some, however, have carried bands (still legible) for 9 yr. Certainly, a number of birds of both species have been recaptured with their original bands illegible due to wear, so that their past histories have been lost. Band loss will, of course, introduce bias in favour of underestimating the survival rates.

iii. The unequal efforts in different years at recapturing the marked populations (with no recapturing at all in some years) introduces a serious bias towards overestimating the survival rates. The negative and poor years (in terms of recapture effort) were mostly before 1957. If a marked population is neglected for some years after initial banding, then birds dying in these early years would have very little chance of being detected; but birds recaptured, say, 5 yr. later must have been alive in those previous years, and thus on paper one is likely to have an apparent 100 per cent per annum survival for this period. This type of bias is apparent in the snow petrel data particularly. Any survival figure is a mean for the population and, if the minimal figures available are incomplete, then the resulting "average" will be over-weighted. On the other hand, there will be some compensation for this, because in the years of inadequate effort birds whose bands were weakened or in the last stages of legibility would "disappear" prematurely.

To some extent (ii) and (iii) will be compensatory but it is not likely they will cancel each other out, and so the survival estimates given hereafter must be regarded as approximations only.

Cape Pigeon (*Daption capensis*)

Of the two species dealt with in this paper, the cape pigeon has the more northerly distribution. It does not breed south of the Antarctic Circle, and its South Atlantic "headquarters" are in the South Orkney and South Sandwich Islands (Kemp and Nelson, 1931; Ardley, 1936; Wilkinson, 1956). The species avoids sea ice and only a small number winters south of the Antarctic Convergence. Outside the breeding season it is pelagic in distribution, undertaking circum-polar migration in the west-wind belt; banded birds have travelled from Signy Island to Chile, New Zealand and the New Hebrides.

Pinder (1966) has given an account of the breeding biology of the cape pigeon on Signy Island. His field work was done in the summers of 1960–61 and 1961–62, and it is largely due to his thorough search for marked birds (especially in 1960–61) that the recapture data are as complete as they are. In the 3 yr. which have elasped since his departure, only three "old" birds not recaptured by him have been traced. Table I shows the annual variation in the recapturing

TABLE I. EFFICIENCY OF RECAPTURING EFFORT OF MARKED CAPE PIGEONS ON SIGNY ISLAND

	Seasons of Recapture													
	1948–49	1949–50	1950–51	1951–52	1952–53	1953–54	1954–55	1955–56	1956–57	1957–58	1958–59	1959–60	1960–61	1961–62
Minimum number of individuals known to have been alive	1	13	6	7	18	42	70	70	121	121	138	136	189	(174)*
Number recaptured	0	11	0	0	5	5	0	23	0	41	51	27	147	160
Percentage recaptured	0	84·7	0	0	27·5	11·9	0	32·8	0	33·9	37·0	20·0	77·8	

* Believed to be incomplete (see text).

effort over 14 seasons; the 1961–62 figure for those still at risk is believed to be incomplete, hence the drop from 189 to 174 despite additional banding the previous summer. Certainly the search for banded birds was less complete in 1961–62, for Pinder was then concentrating on his study area. Only recapturing in later years indicates how many birds were missed in any one season, and only a small proportion has been handled in the three summers since Pinder left Signy Island.

It must be reported that many adults have not been traced in years subsequent to banding. Thus, of 60 adults banded in the 1953–54 summer only 32 were found in later years, and of 82 banded in the 1955–56 summer only 57 were traced subsequently. Of the 46 breeding adults marked in the 1952–53 season, 23 were known to be still alive in the 1960–61 summer, 8 yr. later; this implication of an 88 per cent per annum adult survival will be shown to be much too low. It is difficult to account for the disappearance of the substantial numbers that have not been seen again. Table I shows that during the ten seasons between 1950 and 1959 hardly more than one-third of those at risk were caught in any one year, and usually less than that. As previously mentioned, the soft-temper bands used before 1960 could not be relied upon to last for more than 5 yr. Because of this, it is believed that band loss, aggravated by low recapture effort, is the main reason. It may be that some birds have changed their nest sites, for some nests (particularly on Polynesia Point) are difficult of access; yet the evidence available (Pinder, 1966) suggests that such behaviour is rare.

Table II presents all data for recaptures of breeding adult cape pigeons on Signy Island. For the reason outlined above, the numbers recaptured have not been compared with the numbers originally banded. Thus the survival for the first year after banding cannot be ascertained; however, there is no evidence that banding influences survival, and desertion due to handling is infrequent.

The figures in Table II are subject to the types of bias mentioned on p. 64. Note the apparent 100 per cent survival rate from the second to fifth seasons for those banded in 1952–53, actually due to the fifth season being the most complete search up to then; while the recapture figures for those banded in 1948–49 (band-loss is indicated) tend to underestimate the proportions of survivors. Using all data, the resulting survival estimate is 0·9417 (or 94·17 per cent per annum). Neither here, nor in the other survival estimates given hereafter, are the data considered sufficiently precise for a standard error to be at all meaningful. Survival estimates may be translated into average expectation of further life by the formula $(2-m)/2m$, where m equals the annual mortality. The survival rate of 94·17 per cent is equal to a reproductive life of 16·65 yr.

The faults in Table II arise from the incomplete recapturing effort in the early years. A refinement will be to consider only the data obtained in more recent years when the recapturing was more complete. Table I indicates that the 1957–58 season is the most suitable date line for this purpose, and for this one treats birds banded in earlier years as though in their first season at risk if alive in 1957–58. The data are set out in Table III; the geometrical mean of 0·9493 survival equals 19·22 yr. of adult life.

On Signy Island the banding of cape pigeons has been concentrated in two localities, Factory Cove bluffs and Polynesia Point, the latter being the largest colony. Lest unequal

TABLE II. CALCULATION OF MEAN ANNUAL ADULT SURVIVAL RATE OF BANDED CAPE PIGEONS ON SIGNY ISLAND, USING ALL DATA

Year of Banding	*Known Period of Survival* (yr.) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	*Accumulated Total at Risk*
1947–48	1	1	0											0	1
1948–49	12	4	4	4	3	3	3	2	2	2	2	2	2		13
1949–50	2	2	2	2	0							0			15
1950–51	1	1	1	1	1	0					0				16
1951–52	11	8	7	7	5	5	5	5	4	3					27
1952–53	28	27	27	27	27	26	23	23	19						55
1953–54	32	32	30	30	29	27	25	20							87
1954–55	0						0								87
1955–56	57	57	52	50	48	41									144
1956–57	0				0										144
1957–58	23	22	21	16											167
1958–59	7	7	6												174
1959–60	59	48													233
1960–61	20														253
TOTAL	253	209	150	137	113	102	56	50	25	5	2	2	2	0	
Proportion surviving	$\frac{253}{253}$	$\frac{209}{233}$	$\frac{150}{174}$	$\frac{137}{167}$	$\frac{113}{144}$	$\frac{102}{144}$	$\frac{56}{87}$	$\frac{50}{87}$	$\frac{25}{55}$	$\frac{5}{27}$	$\frac{2}{16}$	$\frac{2}{15}$	$\frac{2}{13}$		
=	1·0	0·8969	0·8622	0·8204	0·7847	0·7086	0·6437	0·5748	0·4544	—— very small sample ——					
If annual survival rate is S, these equal	S	S^2	S^3	S^4	S^5	S^6	S^7	S^8	S^9						
Thus S equals		0·9469	0·9517	0·9517	0·9523	0·9443	0·9391	0·9330	0·9160						
	Geometrical mean $S = 0·9417$														

TABLE III. CALCULATION OF MEAN ANNUAL ADULT SURVIVAL RATE OF BANDED CAPE PIGEONS ON SIGNY ISLAND, USING RECAPTURE DATA SINCE 1957–58 INCLUSIVE

Year of Banding	*Known Period of Survival* (yr.) 1	2	3	4	5	*Accumulated Total at Risk*
1948–49	2	2	2	2	2	2
1949–50	0				0	2
1950–51	0				0	2
1951–52	5	5	5	4	3	7
1952–53	27	26	23	23	19	34
1953–54	30	29	27	25	20	64
1954–55	0				0	64
1955–56	57	52	50	48	41	121
1956–57	0				0	121
1957–58	23	22	21	16		144
1958–59	7	7	6			151
1959–60	59	48				210
1960–61	20					230
TOTAL	230	191	134	118	85	
Proportion surviving	$\frac{230}{230}$	$\frac{191}{210}$	$\frac{134}{151}$	$\frac{118}{144}$	$\frac{85}{121}$	
=	1·0	0·9095	0·8874	0·8194	0·7025	
If annual survival is S, these equal	S	S^2	S^3	S^4	S^5	
Thus S equals		0·9537	0·9610	0·9515	0·9317	
	Geometrical mean $S = 0·9493$					

attention to these two localities has introduced bias (the results suggest it has—see below), the mean annual adult survival for these has been calculated separately, using (as in Table III) the recapture data since the summer of 1957–58 inclusive. Of course, the samples are small when split in this way (99 birds at the bluffs and 121 at the point). These two life tables have not been given in full (this being deemed unnecessary); the results are included in the following summary:

Cape Pigeon Mean Adult Survival Estimates

	Percentage Survival per Annum	*Equivalent Adult Life Span* (yr.)
All data (Table II)	94·17	16·65
All data from 1957–58 (Table III)	94·93	19·22
Factory Cove bluffs; data from 1957–58	94·54	17·82
Polynesia Point; data from 1957–58	95·02	19·58

These four estimates are derived from different facets of the same body of data. It therefore follows that any defects in the data as a whole (additional to those already mentioned) will affect all four estimates.

At present one should not be more precise than to say that the cape pigeon mean annual adult survival rate is approximately 94–95 per cent, which is equivalent to 16–20 yr. of adult life. To this span must be added the period of immaturity, the length of which is not properly known. Down to 1964 there was no evidence that cape pigeons nested while under 7 yr. of age, but when this paper was nearing completion a cable was received from Signy Island stating that five ringed as chicks by R. Pinder in February 1961 were found breeding (but not sexed) in January 1965, at 4 yr. of age. It has yet to be ascertained what proportion begins breeding so early; there is evidence from others of the Procellaridae (cf. Richdale, 1957; Serventy *in* Palmer, 1962) that females begin breeding earlier than males.

It is certain that the British Antarctic Survey banding scheme has not been operative for the potential life span of a cape pigeon. Our oldest birds are two banded as breeding adults (ages not known) in the summer of 1948–49 and still alive in the 1961–62 season, 13 yr. later. However, attention is drawn to the record given by Hennings (1959); a cape pigeon (said to have been "adult" but perhaps a pre-breeder) caught on a German whaler in the Weddell Sea on 7 January 1938 was recaptured (and released) in New Zealand on 5 August 1958, over 20 yr. later.

Snow Petrel (*Pagodroma nivea*)

A more southerly bird than the cape pigeon, the present species breeds widely on the mainland of the Antarctic continent. A few snow petrels nest as far north as South Georgia, but even in winter they are not normally seen north of the Antarctic Convergence. The snow petrel is a characteristic bird of the pack-ice zone, and it is the only petrel regularly recorded in large numbers in inshore waters during the winter months. An account of the breeding biology of this petrel (based on field work in the Ross Dependency) was given by Maher (1962).

Large numbers of snow petrels breed on Signy Island, usually nesting alongside the cape pigeons. The former have received rather less attention from British Antarctic Survey ornithologists than have the latter. Fewer snow petrels have been banded and, as Table IV shows, the data have suffered rather more from inadequate recapturing.

Table IV. Efficiency of Recapturing Effort of Marked Snow Petrels on Signy Island

	Seasons of Recapture													
	1948–49	1949–50	1950–51	1951–52	1952–53	1953–54	1954–55	1955–56	1956–57	1957–58	1958–59	1959–60	1960–61	1961–62
Minimum number of individuals known to have been alive	5	13	17	17	37	36	38	40	52	52	52	52	61	(100)*
Number recaptured	3	4	0	2	12	0	0	4	0	0	4	9	50	89
Percentage recaptured	60·0	30·7	0	11·8	32·4	0	0	10·0	0	0	7·7	17·3	82·0	

* Believed to be incomplete (see text).

Using the same procedure as with the cape pigeon, Table IV indicates the variation of the recapture effort in different years, and Table V presents all the Signy Island data. These reveal the weaknesses of the snow petrel material, which is below the standard of that for the cape pigeon. The apparent 100 per cent survival from year to year is due to the poor recapture effort in the earlier years; a bird alive in 1960 must have been alive in all previous years (back to the season of banding) but, because of the paucity of recapturing before 1958, it is not known how many birds died in the early years. Band loss is believed to have been heavy, aggravated by the low recapture rate, and only a small proportion of those banded have been traced in later years. Thus, of 24 breeding adults marked in the 1949–50 season only 6 were found subsequently, and of 60 banded in 1951–52 only 20 were found in later years; however, of these 20, 15 were still alive in the 1960–61 summer, 9 yr. later. Pinder made a good search for banded birds in 1960–61, but the recapturing in the 1961–62 season was much less complete; hence, for example, the apparent drop from 15 to 9 of those banded in 1955–56.

TABLE V. CALCULATION OF MEAN ANNUAL ADULT SURVIVAL RATE OF BANDED SNOW PETRELS ON SIGNY ISLAND, USING ALL DATA

Year of Banding	*Known Period of Survival* (yr.) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	*Accumulated Total at Risk*
1947–48	5	5	3	3	3	2	2	2	1	1	1	1	1	1	5
1948–49	8	8	8	8	5	5	5	4	4	4	4	2	2		13
1949–50	6	6	6	3	3	3	3	3	3	3	2	0			19
1950–51	0										0				19
1951–52	20	18	18	18	16	16	16	15	15	12					39
1952–53	8	8	8	8	8	8	8	8	5						47
1953–54	2	2	2	2	2	2	2	1							49
1954–55	2	2	2	2	2	2	2								51
1955–56	16	16	16	16	15	9									67
1956–57	0				0										67
1957–58	0			0											67
1958–59	1	1	1												68
1959–60	13	11													81
1960–61	56														137
TOTAL	137	77	64	60	54	47	38	33	28	20	7	3	3	1	
Proportion surviving	$\frac{137}{137}$	$\frac{77}{81}$	$\frac{64}{68}$	$\frac{60}{67}$	$\frac{54}{67}$	$\frac{47}{67}$	$\frac{38}{51}$	$\frac{33}{49}$	$\frac{28}{47}$	$\frac{20}{39}$	$\frac{7}{19}$	$\frac{3}{19}$	$\frac{3}{13}$	$\frac{1}{5}$	
=	1·0	0·9506	0·9412	0·8956	0·8060	0·7015	0·7450	0·6735	0·5958	0·5128	0·3684	0·1579	0·2308	0·2000	
If annual survival rate is S, these equal	S	S^2	S^3	S^4	S^5	S^6	S^7	S^8	S^9	S^{10}	S^{11}	S^{12}	S^{13}	S^{14}	
Thus S equals		0·9750	0·9800	0·9727	0·9579	0·9426	0·9588	0·9517	0·9441	0·9354	0·9133	0·8574	0·8933	0·8515	

Geometrical mean S for the years 2–14 = 0·9356
for the years 2–10 = 0·9574

The factors mentioned above (inadequate recapturing *versus* band loss) will be compensatory to some extent. In Table V, the samples over the last 4 yr. are very small, and because of this two means have been given, one from which these small samples have been excluded.

Because the recapture effort since the 1958–59 season (inclusive) has shown improvement, a life table (Table VI) using only these data has been given. Hence the effects of inadequate recapturing are lessened; the less complete cover in the final year (1961–62) still applies.

TABLE VI. CALCULATION OF MEAN ANNUAL ADULT SURVIVAL RATE OF BANDED SNOW PETRELS ON SIGNY ISLAND, USING RECAPTURE DATA SINCE 1958–59 INCLUSIVE

Year of Banding	*Known Period of Survival* (yr.) 1	2	3	4	*Accumulated Total at Risk*
1947–48	1	1	1	1	1
1948–49	4	4	2	2	5
1949–50	3	3	2	0	8
1950–51	0			0	8
1951–52	16	15	15	12	24
1952–53	8	8	8	5	32
1953–54	2	2	2	1	34
1954–55	2	2	2	2	36
1955–56	16	16	15	9	52
1956–57	0			0	52
1957–58	0			0	52
1958–59	1	1	1		53
1959–60	13	11			66
1960–61	56				122
TOTAL	122	63	48	32	
Proportion surviving	$\frac{122}{122}$	$\frac{63}{66}$	$\frac{48}{53}$	$\frac{32}{52}$	
=	1·0	0·9545	0·9055	0·6153	
If annual survival is S, these equal	S	S^2	S^3	S^4	
Thus S equals		0·9770	0·9677	0·8857	
	Geometrical mean $S = 0{\cdot}9421$				

Of the 137 adult snow petrels used for Table V, 86 were breeding on Factory Cove bluffs and 38 on Polynesia Point. The latter group is too small for separate analysis; using the more recent data only (as in Table VI) a separate figure has been obtained for the Factory Cove bluffs colony (but the table is not given in full).

Snow Petrel Mean Adult Survival Estimates

	Percentage Survival per Annum	*Equivalent Adult Life Span* (yr.)
All data (Table V):		
i. On seasons 2–14	93·56	15·03
ii. On seasons 2–10	95·74	22·85
All data since 1958–59 (Table VI)	94·21	16·77
Data for Factory Cove bluffs; 1958–59 onwards	92·94	13·66

Obviously, the snow petrel data leave much to be desired. It would appear that the average annual adult survival rate falls between 93 and 96 per cent, but these extremes are well separated and equivalent to a mean adult life expectation of between 14 and 24 yr.! As with the cape pigeon, the British Antarctic Survey banding scheme has not been extant for the potential life span of this species. Our oldest snow petrel was marked as a breeding adult (age unknown) in November 1949 and was still alive (and breeding) 15 yr. later, in January 1965.

The period of immaturity of the snow petrel is not known. Very few have been banded as nestlings and as yet none has been found breeding.

Discussion

The limitations of the British Antarctic Survey banding data have been outlined, and approximate mean annual adult survival rates given for the cape pigeon (94–95 per cent) and snow petrel (93–96 per cent).

Pinder (1966) has given the following fledging successes from his marked cape pigeon nests on Signy Island (as in all Procellaridae, normally only one egg is laid):

Season	*Location*	*Number of Marked Nests*	*Percentage Fledging Success*
1960–61	Factory Cove bluffs	25	36
1961–62	Factory Cove bluffs	25	34
1961–62	Polynesia Point	45	
1962–63	Polynesia Point	45	33

Thus over three seasons approximately one-third of the nests studied produced young which reached the fledging stage. If one assumes this to be the average success, and takes into account that a survival rate of 94·5 per cent per annum is equivalent to an adult life expectation of approximately 18 yr. then it will be seen that a hypothetical pair of cape pigeons would during their equally hypothetical 18 breeding seasons together, rear six young to the fledging stage. In a stable population, recruitment to the breeding population equals adult mortality. Thus of the six young reared by our hypothetical pair, two would be required to "replace" their parents and the others would be surplus, to die during the long period of immaturity. In all bird populations studied so far the mortality among young and inexperienced birds is much greater than among adults; an immature mortality rate of two-thirds the total birds fledged (as in the hypothetical case given above) is quite normal. Thus Pinder's data on fledging success for the cape pigeon are quite in keeping with the indicated 94–95 per cent per annum adult survival rate.

Precise data on fledging success are not available for the snow petrel. However, Prévost (1964, p. 101) has given an arbitrary estimate of 55–60 per cent nest failure for the species; this is an assessment based on an incomplete record over two different years (1953 and 1956) rather than a follow-through of a complete breeding cycle. His ecological studies were made in Terre Adélie. Dependent on how accurate Prévost's figure proves to be (more field work is required), then the fledging success of his snow petrels may not be markedly different from

Pinder's cape pigeons. This is not to say that they must have similar adult survival rates; juvenile mortality and deferment of maturity are still largely unknown (and potentially variable) factors for both species.

As yet, little is known of the population dynamics of the Procellaridae. In addition to the adult survival estimates given here for the cape pigeon and snow petrel, five other such figures are available. The most precise adult survival estimate to date for a petrel is that for the northern fulmar (*Fulmarus glacialis*), with $93{\cdot}78 \pm 0{\cdot}75$ per cent per annum, equalling $15{\cdot}58 \pm 1{\cdot}93$ yr. of reproductive life (Dunnet, Anderson and Cormack, 1963). Orians (1958), attempting to give such an estimate for the Manx shearwater (*Procellaria puffinus*), found his data to be non-random; but he considered the annual adult survival to be between 93–97 per cent. Richdale (1963, p. 80–85) believed the survival of his adult sooty shearwaters (*Puffinus griseus*) to be between 92–94 per cent annually. Farner (*in* Palmer, 1962, p. 184) found the minimum adult survival rate for the short-tailed shearwater (*Puffinus tenuirostris*) to be 91 per cent per annum; but the study was made on a colony decreasing in size and he believed that in a stable population the annual adult survival might be as high as 95 per cent. The fifth species, the royal albatross (*Diomedea epomophora*), has the highest mean adult survival rate so far known for a wild bird, approximately 97 per cent per annum, a mean of 36 yr. of adult life (Lack, 1954; from data in Richdale (1952)); however, Richdale's small colony was increasing in size, and so it is possible that his survival figure is a little higher than that for a population that was stable.

It is interesting that all seven adult survival estimates available for the Procellaridae are in excess of 90 per cent per year and usually much higher than that figure, indicating that the larger species (at least) in this family are long-lived, actually as well as potentially. Long adult life and slow reproductive rate (both typical of this group) are familiarly associated with deferred maturity. For example, the royal albatross begins breeding at 8–9 yr. (for females) and 9–11 yr. (for males) (Richdale, 1957, p. 108). Fisher (1952, p. 352), on theoretical grounds, considered that the northern fulmar may not breed until 7–9 yr. old, and support for this has been provided by Aberdeen University, who found two breeding at 7 and 8 yr., respectively (personal communication from A. Anderson). Serventy (1957; *in* Palmer, 1962, p. 183) has ascertained that in the short-tailed shearwater the females begin breeding between 5 and 7 yr., and males between 6 and 8 yr. Richdale (1963, p. 77) considered that the sooty shearwater breeds at 6 yr.; and Dr. M. P. Harris (personal communication) has said that the Manx shearwater commonly breeds at 5 and has once been found nesting at 3 yr. old. The British Antarctic Survey banding data suggest that the giant petrel (*Macronectes giganteus*) begins to breed at 6 yr. (based on four records), and (as previously mentioned) the cape pigeon does so at 4 yr.

Unfortunately, there are no adult survival estimates for the smaller species of petrel. Richdale (1949, 1952) found his common diving petrels (*Pelecanoides urinatrix*) breeding at 2 yr., and Gross (1947) had a Leach's petrel (*Oceanodroma leucorrhoa*) nesting (but possibly not for the first time) at 3 yr. It is to be expected that these smaller species, having shorter periods of immaturity, will experience higher population turn-over than the species previously mentioned. It remains to be seen, when further data are available, to what extent the three parameters of size, period of immaturity, and adult survival are correlated.

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