FOOD, MOULT AND AGE OF FIRST BREEDING IN THE CAPE PIGEON, Daption capensis Linnaeus

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ABSTRACT. The food and feeding habits of the cape pigeon at Signy Island are described from regurgitated food samples and direct observations. A few fish and several deep-water Crustacea were present in the samples but krill (*Euphausia superba*) was by far the most important constituent.

The sequence and timing of the moult are discussed in relation to the breeding cycle. Birds freed from breeding responsibilities by loss of their egg or chick apparently start wing moult before successful breeders and this probably begins between 10 and 17 February, as the young near fledging. The large outer primaries are renewed at sea during a 'moult exodus' from the island in late February/early March, following departure of the young. Primary moult is estimated to last about 85 days. Rapid synchronous moult of the rectrices, which begins as primary replacement nears completion, may allow the entire moult as well as breeding to be completed within the short summer period of maximum food availability. During tail moult, the flight function of the rectrices appears to be temporarily assumed by the unusually long tail coverts.

Recent ringing records indicate that most birds do not breed until they are at least 5 years old, and that adults and young winter off the Chilean coast.

This paper is mainly concerned with some observations on the food and moult of the cape pigeon (*Daption capensis*) at Signy Island (lat. 60°43′S., long. 45°38′W.), South Orkney Islands, and it is intended to supplement the recent detailed study of the annual cycle and breeding biology of the species at Signy Island by Pinder (1966). In addition, further records of the age of first breeding which have accumulated since the completion of Pinder's study are included.

The work was carried out during the seasons 1965–66 to 1967–68 in the cape pigeon colonies described and studied by Pinder at Factory Cove bluffs (50 pairs) and in Polynesia Point gully (about 1,000 pairs). Although the information is not complete, certain features are sufficiently clear to justify preliminary discussion and to indicate that further long-term study of this abundant and distinctive Antarctic species would be most rewarding.

Cape pigeons return to form breeding colonies at Signy Island in September/October and egg-laying, which is closely synchronized, takes place during the last week of November and first week of December. As will be shown, breeding and moult overlap to some extent; body moult begins during incubation and moult of the primaries apparently begins before the young fledge at the end of February.

FOOD AND FEEDING

Most references to the food and feeding habits of the cape pigeon have described only the well-known scavenging behaviour from observations made during whaling voyages or around shore stations. The importance of carrion in the diet may thus have been over-emphasized and knowledge of the normal food taken at sea is limited to isolated observations of feeding dividuals, supplemented by stomach-content analyses of a few birds which were not members scavenging flocks.

Both adult and young cape pigeons eject oil and regurgitate their stomach contents when disturbed on the nest; this semi-digested food often includes identifiable remains, e.g. euphausid Crustacea (Clarke, 1906; Ardley, 1936). The present information on the food of the cape pigeon at Signy Island is based mainly on a collection of nine regurgitated food samples taken from adults and 85 samples from chicks in January/February 1966. Samples were collected by means of a large (20 cm. diameter) polythene funnel mounted on a stick, the regurgitated material being retained in polythene bags tied to the neck of the funnel. Adults or their young were approached to within 1 m. and the funnel was held under the bill. Regurgitation usually followed immediately and the bird was then gently prodded until no more food was produced. Recognizable remains were recovered from birds which had recently fed; individuals which had presumably not fed for several days produced only a thin greenish liquid containing little solid material and these samples were discarded. At first, attempts were made to keep samples separate but rapid solidification of the oily food made this impracticable. However, it was soon apparent that the major constituent was krill (Euphausia superba) so that samples could be

sorted in the field. Only representative specimens of krill were retained together with any material which could not be identified immediately. This procedure may have caused underestimation of some small items, e.g. fish eye-lenses, but it is unlikely to have been an important source of error. The constituents of samples taken from incubating adults did not differ from those taken from brooding adults or the young, and the records have been combined.

The results set out in Table I show that *Euphausia superba* is by far the most important food species and it probably constitutes the staple diet of the cape pigeon at Signy Island throughout the summer. Most were adult specimens but adolescent and furcilia stages also occurred. The surprisingly small range of other species suggests that these may be taken only incidentally. The fish remains, found in 16 per cent of the samples and consisting of eye-lenses and sections of vertebral columns, have not been identified but they probably refer to pelagic nototheniid species such as *Pleuragramma*. The size of these remains indicated that the fish were approximately 5–10 cm. long.

Table I. Prey found in 94 food samples from cape pigeons at Signy Island

Food species		Percentage frequency of occurrence
Fish		
Unidentified		15.9
Crustacea		
Euphausiacea	: Euphausia superba	97.9
Mysidacea: G	nathophausia spp.	1 · 1
Amphipoda:	Eurythenes spp.	4.2
	Cheirimedon femoratus	2·1
	Lepidepecreum cingulatum	1 · 1
	Oradarea spp.	1 · 1
	Pontogeneiella brevicornis	2·1
Isopoda: Anu	uropus antarcticus	2 · 1
Tunicata Unidentified s	alp	1.1
Mollusca		
Pteropoda: C	Clione antarctica	1.1

The small amphipods, Cheirimedon femoratus, Oradarea spp., Lepidepecreum cingulatum and Pontogeneiella brevicornis, which are common in the sub-littoral zone at Signy Island, were present in only two samples taken from adults at Polynesia Point gully on 8 February 1966. Throughout that day, 200–300 cape pigeons were actively swimming and feeding close to two large ice floes which, driven by wind, had grounded in Factory Cove. The birds were tightly packed, jostling for position and rapidly picking objects from the surface, as well as up-ending for deeper prey. The rocking action of the ice in the heavy swell had disturbed or injured many amphipods in the weed and stones on the sea bed in the cove, bringing them up within reach of the waiting petrels. This method of feeding was observed on several other occasions—whenever strong easterly winds caused large floes or bergy bits to ground in the shallow water

of Borge Bay. Floes which were still drifting before the wind were ignored by the birds on the occasion described.

The most unexpected constituents of the samples were two Anuropus antarcticus, an isopod previously known only from one specimen found in a snow petrel (Pagodroma nivea) stomach (Hale, 1952), four examples, 6-7 cm. long, of the very large amphipod Eurythenes spp. (E. gryllus or possibly E. magellanicus (personal communication from M. H. Thurston)) and a single specimen of the mysid Gnathophausia spp. (probably G. gigas (personal communication from Dr. O. S. Tattersall)). Some of these specimens, the *Eurythenes* and *Anuropus* particularly, were in relatively good condition and were most probably caught alive by the birds. These Crustacea are generally considered to be deep-water forms and their presence in the diet of a surface-feeding petrel is not easy to explain. It seems likely, however, that they perform extensive vertical migrations to and from the surface layers and become available to feeding petrels more frequently than has been suspected. Certainly, the amphipod Eurythenes must be captured fairly regularly as specimens were recorded in samples in 1966 and again in 1968. None of these crustaceans had been recorded previously from inshore waters at Signy Island, nor do they appear numerous in the extensive pelagic collections made during the Discovery Investigations in the Scotia Sea. These records thus provide additional evidence that oceanic pirds are able regularly to catch organisms only occasionally represented in routine plankton auls made in the same area (Tickell, 1964).

It is evident from the few published accounts that the prey of the cape pigeon varies considerably with locality, Crustacea being important in some places, while in others squid are favoured. Murphy (1936) stated that remains of fish, Crustacea and squid have been found in stomachs of birds taken away from shore stations or whaling/sealing operations. Two stomachs of birds he collected off Peru contained 500 or more *Emerita analoga*, an anomuran decapod usually associated with the wave-wash zone of sandy shores rather than the open sea, while a third bird in the same area contained squid beaks, gravel and laminate weed. Falla (1937) reported cephalopod beaks in two birds taken from nests in Enderby Land, while Gain (1914) found euphausids in one stomach at the Petermann Islands, off Graham Land. At Heard Island, cape pigeons have been seen feeding on the siphonophore *Pyrostephos vanhoffeni* and on swarms of the euphausid *Thysanoessa vicina* washed close inshore (Downes and others, 1959). Crustacean swarms are rarely observed in inshore waters at Signy Island but they occur fairly frequently at Deception Island, South Shetland Islands, where they attract large numbers of cape pigeons and also Antarctic terns (*Sterna vittata*).

More quantitative information has been provided by Bierman and Voous (1950) from stomach analyses of 17 birds collected at sea in the eastern South Atlantic. From the large number of beaks and eye-lenses found, they concluded that the normal food at sea consists chiefly of cephalopods (present in 88 per cent of stomachs examined), followed by Crustacea (47 per cent occurrence), fish (24 per cent) and pteropods (6 per cent). Although squid are undoubtedly eaten regularly, they are perhaps less important than these results suggest, for their small indigestible remains may accumulate in the stomach over a long period.

Feeding range

It is not known how far cape pigeons normally fly from the breeding colonies in order to feed. At Signy Island, inshore feeding is relatively unimportant and evidently most of the food is obtained at sea away from the island. The incubation spells of 4–5 days (Pinder, 1966) are consistent with this view as, during this time, birds could fly over 640 km. from the island, judging from homing experiments carried out with other petrels (Matthews, 1953; Billings, 1968). Bierman and Voous (1950) collected a female cape pigeon in breeding condition about 355 km. from the nearest colony, Bouvetøya, while other adults were found up to 1,860 km. from land. Some of the latter, however, were in wing moult and were almost certainly failed breeders, i.e. birds which had lost their egg or chick (see p. 39).

Although Signy Island birds may fly considerable distances in order to feed, there is evidence that at Heard Island food may be abundant in inshore waters. Falla (1937) encountered large flocks of scavenging individuals there and he considered most were non-breeders. Downes and others (1959) described flocks frequently feeding close inshore at the edge of the surf,

presumably on organisms stirred up by the breaking waves. Furthermore, both authors stated that dove prions (*Pachyptila desolata*) often feed close inshore at Heard Island—a habit unknown in the dove prion at Signy Island (Tickell, 1962).

Scavenging

The scavenging habits of the cape pigeon have been summarized by Murphy (1936). During the present study, birds were seen readily to be attracted to seal blubber and other fatty material floating on the sea surface. They quickly gathered to feed on scraps left after penguins had been killed by leopard seals (*Hydrurga leptonyx*) or after attacks upon seals by killer whales (*Orcinus orca*). Dead or dying birds of any species on land were ignored but, on several occasions, cape pigeons were seen to leave the water to feed on dead nototheniid fish lying on the beach below the British Antarctic Survey station.

MOULT

Murphy (1936), summarizing what was known of the moult in the cape pigeon, concluded that "the moult of the quill feathers takes place during the rearing of the chicks" and that "feather replacement continues until April or May". Detailed information in support of Murphy's conclusions has been given by Bierman and Voous (1950), who examined a number of moulting individuals collected at sea during the breeding season, and also by Stresemann

and Stresemann (1966) in their comprehensive review of moult in birds.

The moult records discussed in this paper were obtained in 1966–67 and 1967–68 while checking the ring numbers of occupants of marked nests in Pinder's study colonies. As the breeding cycle of the cape pigeon is highly synchronous and its start is constant from year to year (Pinder, 1966), records for the two seasons have been combined. Every bird handled was examined for moult of the primaries and, if time allowed, details of tail, secondary and body moult were also noted; all data were recorded on cards provided for this purpose by the British Trust for Ornithology.

Method of recording moult

A simple, standard numerical system is necessary for precise description of the moult process and the method employed was essentially that used by Ashmole (1962) in his studies of tropical terns. Individual flight feathers were allotted a score according to stage of development, thus 0 indicated an old feather remaining; 1 a feather missing or in pin; 2, 3 and 4 new feathers up to one-third, two-thirds or almost full grown, respectively; 5 new feather fully grown. Summing the scores of individual feathers in a feather group gave a total score, which provided an index of the stage which moult had reached in that group. For example, the primary moult score for a bird having just completed replacement of all its primaries would be 100 (10 new feathers each scoring 5 in each wing) and the equivalent tail-moult score would be 70 (14 new tail feathers). The scores, both for individual growing feathers and for groups of feathers, are almost directly proportional to the date and allow estimates of the timing and duration of the moult to be made (Evans, 1966; Newton, 1966). The moult of the vestigial eleventh primary was not recorded.

Moult of the body feathers

In the Signy Island breeding population, moult begins with the body feathers in the last week of December during incubation, when shed contour feathers begin gradually to accumulate around the nests. Body moult during incubation is also known in the giant petrel (Macronectes giganteus) (Warham, 1962), short-tailed shearwater (Puffinus tenuirostris) (Marshall and Serventy, 1956), white-headed petrel (Pterodroma lessoni) (Warham, 1967) and snow petrel (Pagodroma nivea) (paper in preparation by J. R. Beck). Both non-breeding immature birds and successful breeders were noted still having many actively growing body feathers at the beginning of April. The contour feathers of the cape pigeon may constitute as much as 75–80 per cent of the weight of the entire plumage, judging from the results of Newton (1966) for the bullfinch (Pyrrhula pyrrhula) and Holmes (1966) for the dunlin (Calidris alpina),

and it is perhaps not surprising that their renewal appears to be a gradual process extending over at least 4 months, overlapping about half the incubation and the whole of the nestling period. The overall colour and plumage pattern of this species is appreciably altered by moult and wear as discussed by Murphy (1936). The individuals with pale backs and wings found in low latitudes during the breeding season appear to have a different moult regime from that of established breeders and they are presumably immatures less than 4 years old (see p. 42).

Moult of the primaries

Renewal of the primary feathers in the cape pigeon follows the normal pattern, beginning with the innermost (first) primary and progressing outward from the carpal joint, with up to four outer feathers growing simultaneously. In some species, e.g. the bullfinch (Newton, 1966) and black noddy (Anous tenuirostris) (Ashmole, 1962), the primary moult extends over the entire moult period and it can be used as an index of moult in all feather sets. In the cape pigeon this is not so, as body moult begins before primary moult starts and tail moult continues after its completion. Primary moult scores for all birds found in wing moult at Signy Island from January to April are shown in Fig. 1 where they are plotted against date; hatching

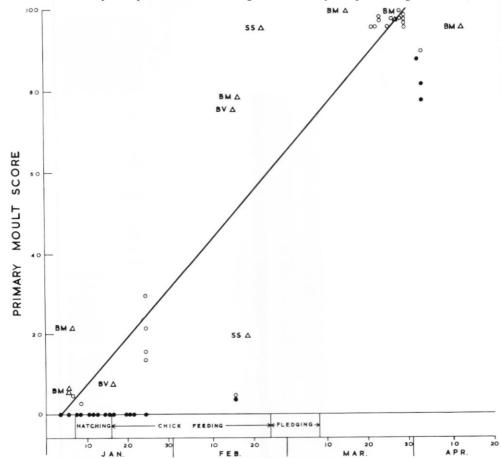


Fig. 1. Primary moult scores of cape pigeons in relation to date and the breeding cycle.

Failed breeder/non-breeding immature.

Successful breeder.

Data from British Museum (Nat. Hist.) specimen (BM), Bierman and Voous (1950) (BV) or Stresemann and Stresemann (1966) (SS). and fledging periods from Pinder (1966) are also included for comparison. Data from seven birds in primary moult (in the collection at the British Museum (Nat. Hist.)), from two birds illustrated by Bierman and Voous (1950) and from two specimens in the American Museum of Natural History (details given by Stresemann and Stresemann (1966)) are also shown.

During December, 34 ringed incubating birds and ten non-breeders or failed breeders and ringed immatures were examined but none was found to be moulting. None of the 102 successfully breeding adults caught at intervals throughout January was in moult but six out of 13 birds at empty nests were in the early stages of primary moult. Of these, a bird of unknown breeding status caught on 7 January had lost the three innermost primaries of each wing, and a failed breeder caught on 9 January was in similar condition. The other four birds resting on empty nests on 25 January were in more advanced stages of primary replacement. Unfortunately, no breeding adults were examined after 27 January and the only February records obtained were from 12 birds on 16 February from a flock resting on the sea in Factory Cove. Ten of these had complete sets of old feathers but two were just beginning to shed the innermost primaries—one was a successful breeder with a chick in a marked nest on Factory Cove bluffs.

The non-breeding section of the population of cape pigeons at Signy Island decreases gradually during the last week in February and there is a total exodus of both breeding adults and non-breeders from the island at the end of the first week in March, immediately following the fledging of the young (Pinder, 1966). After 16 March, the non-breeding population gradually returns and by the end of the month many birds are visiting nests in the colonies, when they can again be recaptured. The successful breeders return later after a longer absence of about a month (first seen 4 April 1962 (Pinder, 1966), 2 April 1968 (personal observations)), and only a few return and re-occupy their old sites, staying until the end of April. Final departure depends on sea-ice conditions but birds of unknown status are often present throughout May.

Sixteen birds were caught, shortly after their return from the post-breeding exodus, between 22 March and 2 April 1968, and all were in the final stages of primary replacement (Fig. 1). Of these, four were unringed and therefore of uncertain status (primary scores 96, 98, 98, 98), six were ringed immatures between 3 and 7 years old and most of which had almost certainly not bred that season (scores 98, 98, 100, 98, 96, 96), three were failed breeders (scores 98, 96, 90) and three were adults which had successfully reared chicks to fledging earlier (scores 88, 82, 78).

The time-table for primary moult indicated by the Signy Island records is supported by the scores for seven moulting birds in the British Museum (Nat. Hist.) collections. Two of these, taken together from a nest at Deception Island, South Shetland Islands, on 6 January were just starting primary moult (scores 6), while a bird taken at Ile de la Possession, Iles Crozet, on 7 January had six inner primaries growing simultaneously (score 22). A much later stage is represented by an individual collected at sea east of the Antipodes Islands, Pacific Ocean, on 17 February (presumably from the breeding population there); the four outer primaries were in active growth (score 79). Two birds collected at sea east of Heard Island on 16 and 28 March had virtually completed primary replacement (scores 100 and 98, respectively), as had a female collected at South Georgia on 13 April (score 96).

Stresemann and Stresemann (1966) have given details of two moulting cape pigeons in the American Museum of Natural History collections. These were collected near the Antipodes Islands and are of particular interest for, whereas one taken on 19 February has a low primary score (about 20), the other taken only 4 days later had almost finished renewing the primaries (score 96).

Finally, additional information has been provided by Bierman and Voous (1950). They stated that birds with moulting inner primaries and secondaries were first noted on 28 December but were not regularly observed until after 4 January. Individuals collected in the period January–March had replaced the inner primaries and the outer ones were either old or still growing, whereas all April birds and one on 20 March had fresh sets of primaries. Some birds collected on 16 February had extremely short outer primaries, which reduced the wing lengths by as much as 20 per cent (see also Murphy, 1936). Diagrams given by Bierman and Voous

39

(1950, p. 68) compare wings of birds taken on 17 January and 16 February, and they are sufficiently detailed to allow primary scores to be allotted to these specimens. These scores are included in Fig. 1; the score for the February bird is very close to that of the British Museum

(Nat. Hist.) specimen taken on 17 February in the Pacific Ocean.

These observations suggest that, as in the fulmar (Fulmarus glacialis) (Wynne-Edwards, 1939) and snow petrel (paper in preparation by J. R. Beck), wing moult in failed and non-breeders takes place considerably earlier than in successful breeders. No successful birds were in wing moult up to the end of January, while one bird with a chick had just begun to renew the inner primaries on 16 February. If this record is representative, then successful breeders begin primary moult between 1 and 24 February (the date of fledging of the first chicks) and probably during the period 10–17 February, when chicks reach peak weights 35 days after hatching (Pinder, 1966). This conclusion is supported by the April records from successful breeders which were less advanced than the failed breeders/immatures. Furthermore, whereas all birds which had failed in incubation were at the same stage as non-breeding immatures, one bird which had lost a well-grown chick to a brown skua (Catharacta skua lönnbergi) was only a little further advanced in wing moult than the three successful birds which fledged chicks.

Although the total available data do not warrant statistical treatment (see Evans (1966) for egression analysis of moult data), the approximate duration and rate of the primary moult can be estimated. From the slope of the line fitted by eye (Fig. 1) for the more complete observations on the failed/non-breeding section of the population, the average rate of increase in primary score is 1·17 points/day, which gives 85 days as a mean figure for the duration of the primary moult.

Moult of the secondaries and tail

No birds handled at Signy Island in January or February appeared to be moulting secondary feathers but, as it proved difficult to distinguish between new and old full-grown feathers and specific checks on secondaries were not often made, some moult may have been overlooked. Seven records of birds in active secondary moult were obtained in March/April 1968 and details are given in Table II. A further seven birds, mostly immatures, examined between 24 and 30 March, showed no secondary moult and had presumably finished. According to Bierman and Voous (1950), moult of the secondaries proceeds irregularly but it starts simultaneously at each end of the series; there is a central subordinate moult locus situated at about secondaries 5–7. The Signy Island records suggest some differences from these conclusions but unfortunately there are too few for adequate discussion. The secondary moult is probably completed at the same time as or before that of the primaries but more work is necessary before its sequence, rate and duration can be established.

The tail moult of the cape pigeon is particularly interesting as the rectrices are shed almost simultaneously (Murphy, 1936); the only other petrel species in which this occurs appear to be the snow petrel and Antarctic petrel (*Thalassoica antarctica*) (Bierman and Voous, 1950). Moult of the tail feathers in the cape pigeon begins as the primary moult nears completion and growth of the new feathers appears to be rapid (Table III). After the rectrices are shed in *Daption* and *Thalassoica*, the tail is represented only by the very long upper and lower tail coverts until the growing quills emerge between them. As Bierman and Voous (1950) have commented, however, loss of the tail does not appear to handicap the flight, and at Signy Island tail-less cape pigeons were observed taking off and alighting at nesting ledges with little apparent loss of manœuvrability. Any loss is presumably adequately compensated in these species by the long tail coverts, which, although lacking the length of the rectrices, preserve the width of the tail, a factor which Evans (1966) suggested might be important in manœuvring.

Discussion

Several points of interest arise from these observations. It seems clear that the post-breeding exodus of the cape pigeon is closely associated with the primary moult; birds have just begun wing moult prior to departure, while those caught immediately on return have almost completed primary replacement. A similar "moult exodus" probably occurs in the snow petrel

Table II. Secondary moult scores of Cape Pigeons at Signy Island in March/April 1968

Date	Breeding status	Primary								Secon	ıdarie	S								
Date	Dreeding status	score	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1
22 March	5 yr. immature	96					1		,									1		
2 March	?	96					3											3		
4 March	?	98					4	,												
6 March	5 yr. immature	96					3	2	5	5	5	5	5	5	5	5	4	4	3	(
0 March	Failed breeder	96					4	4	5	5	5	5	5	5	5	5	3	4	4	(
2 April	Successful breeder	88					3	2	5	5	5	5	5	5	5	5	5	5	5	
3 April	Successful breeder	78				2	0	1	0	2	0	3	4	4	4	4	0	0	1	2

Secondaries marked by a dot could not be designated as either old or new feathers.

Table III. Tail-moult scores of cape pigeons at Signy Island in March/April 1968

D	Donalisa atau	Primary	Rectrices													Total	
Date	Breeding status	score	7	6	5	4	3	2	1	1	2	3	4	5	6	7	score score
22 March	?	96	3	3	3	3	3	2	3	3	2	2	3	3	3	3	39
22 March	5 yr. immature	96	1	1	1	1	1	0	0	0	0	1	1	1	1	1	10
24 March	?	98	2	2	2	2	2	2	3	3	2	2	3	2	2	3	32
24 March	?	98	2	1	2	0	1	1	2	2	1	1	2	1	1	2	19
26 March	5 yr. immature	96	1	0	0	1	1	0	1	0	0	0	1	0	0	1	6
27 March	3 yr. immature	98	3	2	2	2	2	2	2	2	2	2	2	2	2	3	30
29 March	?	98	3	2	3	3	3	1	2	1	3	3	3	3	2	3	35
29 March	3 yr. immature	100	0	3	3	3	3	3	4	4	3	3	3	3	3	4	42
30 March	Failed breeder	98	3	2	2	3	0	1	3	3	1	1	2	2	1	3	27
30 March	7 yr. immature	98	2	1	3	3	1	2	3	3	1	3	2	3	1	2	30
30 March	6 yr. immature	98	3	3	3	3	3	3	4	4	2	3	3	3	3	3	43
30 March	Failed breeder	96	2	0	2	2	2	0	0	2	0	2	2	0	0	2	16
2 April	Successful breeder	88	1	0	0	1	0	0	1	0	0	0	1	1	0	1	6
3 April	Successful breeder	78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Rectrices are numbered in pairs from the centre of the tail outwards.

(paper in preparation by J. R. Beck), while Richdale's (1965) observations suggest that the post-breeding departure and return of diving petrels (*Pelecanoides urinatrix*) and broad-billed prions (*Pachyptila vittata*) (but not narrow-billed prions (*P. turtur*)) at Whero Island, New Zealand, may also be linked with the moult.

Primary replacement presumably imposes a considerable extra physiological strain on the bird additional to that already imposed by body-feather renewal. Hence, during this "moult exodus", birds probably move to more distant rich feeding grounds in order to replenish their reserves. Alternatively, however, it has been implied that their capacity for flight (and therefore for finding food) might be impaired during the moult by the simultaneous growth of three-four arge outer primaries and corresponding reduction in wing length already mentioned (Murphy, 36; Bierman and Voous, 1950). Evidence for impaired flight is slight, resting only on the inconclusive observations by Borchgrevink (1901) on 30 December 1898 that "The Daption capensis was in the midst of moulting and was flying with some difficulty" and by van der Lee (quoted by Bierman and Voous, 1950), who noted that moulting individuals on 28 December did not fly as well as non-moulting birds. But in late December, as shown earlier, only inner primaries are being renewed and their loss was not observed to affect the flight of birds at Signy Island. Moreover, in latitudes renowned for bad weather, even slight incapacity could be dangerous for a species which feeds at the sea surface. Indeed, the need to maintain efficient flight for feeding during moult is probably the most important factor controlling the number of primaries which can be renewed concurrently without ill effect, and thus, together with the rate of growth of individual feathers, this may ultimately determine the duration of the primary

Considerable overlap between moult and the breeding cycle is known in several species which moult on the breeding grounds in the brief Arctic summer, e.g. the Steller jay (*Cyanocitta stelleri*) (Pitelka, 1958), glaucous gull (*Larus hyperboreus*) (Johnston, 1961) and dunlin (Holmes,

1966). The timing of these events in Antarctic species other than penguins has been little studied but Murphy's (1936) statement that moult and parental care in the cape pigeon are concurrent is confirmed and amplified by the present observations. Furthermore, moult information for Pagodroma, Fulmarus, Thalassoica and Macronectes, given by Bierman and Voous (1950), clearly shows that in these petrels also, part of the population is in primary moult when eggs or young are in the nests while, as already mentioned, Pagodroma and Macronectes begin body-feather renewal during incubation. The timing of moult in relation to breeding in these other Antarctic fulmarine petrels may therefore be closely similar to that in the cape pigeon. In both Arctic and Antarctic species, overlap between moult and breeding presumably allows these processes of high energy demand to be fitted into the short summer period when food supplies reach a seasonal maximum. However, the situation is not a simple one for, in the smaller Antarctic Procellarii, only those species which lay in synchrony early in the season undergo a post-breeding moult on the breeding grounds (Beck, in press). Furthermore, factors such as laying date and laying synchrony may be related in turn to body size and nest site. The hole-nesting nocturnal petrels, Wilson's petrel (Oceanites oceanicus), black-bellied storm petrel (Fregetta tropica) and dove prion, have late and extended breeding seasons adapted to snow conditions at the nest and the young fledge from late March to early May. In contrast, in the larger cape pigeon and snow petrel which are less affected by snow conditions, breeding seasons are early and highly synchronized, features which enable the young to fledge by the end of February. Thus, in the latter group but not in the former, there is sufficient time to allow moult to be completed after breeding and before food supplies begin to decline in mid-April (Foxton, 1956). Nevertheless, the margin may still be quite narrow in successful breeders, for the primary moult, whose rate is presumably fixed by the need to maintain flight efficiency throughout the moult period, may not be completed until mid-April. The simultaneous renewal of the rectrices may be adapted to this situation, allowing the moult to be compressed into a shorter period, throughout which the unusually long covert feathers temporarily take over the flight function of the tail quills.

AGE AT FIRST BREEDING

Since the start of the ringing programme at Signy Island in 1947 and up to March 1967, 4,589 cape pigeons have been ringed as nestlings, mostly in the Factory Cove bluffs and Polynesia Point gully colonies. Before 1960, soft-temper aluminium-alloy rings were used but these suffered badly from sea-water corrosion and abrasion on rock. Only small samples of nestlings were ringed in these early years and probably ring loss coupled with inadequate recapture effort accounts for the very small number of recaptures from these year groups. In 1960, tougher monel-metal rings supplied by the British Trust for Ornithology were introduced and ringing of much larger samples was begun by Pinder. Considerable improvement in the number of recaptures followed and about 500 nestlings are now ringed annually as routine in these colonies. Details of recaptures up to and including the 1964–65 season have been given in Pinder's (1966) paper and they show that 4-year-old cape pigeons can rear young (five records) while non-breeding 1–4-year-old birds are present around the breeding grounds in the prolaying period and again in April, i.e. after the "moult exodus".

In the following three seasons, the two colonies were fairly thoroughly searched for birds ringed as nestlings and a further 37 individuals were found breeding while 11 non-breeding and breeding birds were found at North Point, where they had been originally ringed in 1961–63. The age distribution of all birds when first recaptured definitely breeding, i.e. with egg or chick, is given in Table IV. One 3-year-old bird has been found breeding but this is evidently unusual. Although a few birds may have bred undetected in earlier years, it appears that Pinder (1966) stated correctly that cape pigeons may breed at 4 years but the majority may not do so until a year later. These results are similar to those obtained for other Procellaridae of comparable size. Manx shearwaters (*Puffinus puffinus*) have once been recorded breeding at 3 and 4 years but the majority do not breed until at least 5 years old (Harris, 1966), while the short-tailed shearwater begins breeding at 5–7 years (females) and 6–8 years (males) (Serventy, 1957; Palmer, 1962). No cape pigeons of known age have yet been sexed so it is not known whether a similar sex difference in breeding age occurs in this species.

Table IV. Numbers of cape pigeons of known age found breeding at Signy Island in different seasons

Season	Age (yr.)											
	2	3	4	5	6	7	8	9	10	10+	- Total	
1959–60							1				1	
1960-61							1	3			4	
1961–62									2		2	
1962-63											0	
1963-64											0	
1964–65			5							3	8	
1965–66		1	3	7						3	14	
1966–67				5	3		1			3	12	
1967–68				4	10	6				2	22	
Totals		1	8	16	13	6	3	3	2	11		

The highest recapture rate for year groups in the Polynesia Point gully colony is 5·8 per cent surviving to recruitment from the nestling cohorts of 1951–52 (87 ringed) and 1960–61 (276 ringed). This is, as Pinder (1966) pointed out, a minimal figure which is depressed by ring loss, occupation of inaccessible sites within the natal colony and by movement elsewhere. Movement to other colonies is probably the most important of these factors for seven (25 per cent) out of 28 breeding known-age birds in the gully colony, and five out of ten at the Factory Cove colony were fledged from colonies elsewhere on the island, the furthest movement being 4·8 km. from North Point to the gully colony. Nevertheless, an annual recruitment rate of 5·8 per cent may be enough to offset the 5–6 per cent estimated annual mortality of adults (Hudson, 1966), which is also a minimal figure.

As yet there is too little information to be able to compare the breeding performance of birds of known age with that of older individuals. Six of the eight 4-year-old breeders were found with young, while a 4-year-old paired with an established adult reared a chick at the first attempt, as did two 6-year-old birds which, although apparently paired, did not lay in the two previous seasons. Egg loss, however, is known to be high during the first 8 days after laying (Pinder, 1966) and an unknown but possibly higher proportion of eggs may be lost by inexperienced birds which are starting to breed. Thus, unless nests are observed closely from aying onward, results will be very considerably biased toward success. Most 4-6-year-old birds recovered at empty nests in December/January were very probably failed breeders and not birds prospecting future breeding sites.

Apart from the two recoveries of nestlings in their first year in Chile (lat. 32°S.) and the New Hebrides, reported by Pinder (1966), there is now one record of a bird recovered in its third winter near Ancud, Chiloe Island, Chile (lat. 41°S.), while two adults have been recovered, also in Chile during the southern winter, near Talcahuano (lat. 36°S.) and near Tocopilla, Antofagasta (lat. 22°S.). It thus appears that both adult and young cape pigeons from the Signy Island population may winter in the area of cool currents along the western seaboard of South America.

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