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Order PROCELLARIIFORMES

A rather distinct group of some 80–100 species of pelagic seabirds, ranging in size from huge to tiny and in habits from aerial (feeding in flight) to aquatic (pursuit-diving for food), but otherwise with similar biology. About three-quarters of the species occur or have been recorded in our region. They are found throughout the oceans and most come ashore voluntarily only to breed. They are distinguished by their hooked bills, covered in horny plates with raised tubular nostrils (hence the name Tubinares). Their olfactory systems are unusually well developed (Bang 1966) and they have a distinctly musky odour, which suggest that they may locate one another and their breeding places by smell; they are attracted to biogenic oils at sea, also no doubt by smell. Probably they are most closely related to penguins and more remotely to other shorebirds and waterbirds such as Charadriiformes and Pelecaniiformes. Their diversity and abundance in the s. hemisphere suggest that the group originated there, though some important groups occurred in the northern hemisphere by middle Tertiary (Brodkorb 1963; Olson 1975).

Structurally, the wings may be long in aerial species and shorter in divers of the genera *Puffinus* and *Pelecanoides*, with 11 primaries, the outermost minute, and 10-40 secondaries in the Oceanitinae and great albatrosses respectively. The tail varies in length, being forked in *Oceanodroma*, forked to pointed in other forms, usually with 12 rectrices but up to 16 in fulmars. The tarsi are light and cylindrical in aerial forms; strong and laterally compressed with legs set far back in aquatic ones. The front toes are webbed; hind toe small or absent. The proventriculus is long and glandular; the gizzard small and twisted; and the small intestine often spiral in *Pterodroma*, presumably to aid absorption of the unusual lipids in their food. Chicks are helpless and covered in down, with two coats except in some Oceanitinae. Some larger species have a darker immature plumage, and the female is often darker than the male in the great albatrosses. The male is usually larger than the female, though smaller in the Oceanitinae and some other small species. Otherwise there is little difference in appearance with sex or age, except that young birds may have more pronounced pale or dark edges to the feathers. Many have simple counter-shaded markings that often appear to have given rise to uniformly dark or, less often, to pale derivatives; some species in most groups are dimorphic or polymorphic. The more complex groups have often developed distinctive markings of the extremities.

Breed more or less colonially on offshore islands, coastal cliffs, or on hills and deserts inland, where they perform complex vocal and aerial displays. The nest is a simple scrape or cup in a burrow or natural hole, sometimes under vegetation. The s. albatrosses build large cone-shaped nests in the open; may be lined with any debris available in the area. Smaller species visit it only at night, though larger ones and those breeding on remote islands may come to nests in the open by day. Parents incubate for spells of several days in turn and generally leave the chick alone soon after it hatches, only returning at long intervals to feed it by regurgitation. In consequence the chick is vulnerable to introduced predators and some species are now greatly reduced and at least two are now extinct. Some species also periodically liable to have unsuccessful breeding seasons. Many young or even old birds may be wrecked ashore and die when they meet bad weather or suffer shortage of food on migration or in the winter. Though it has been claimed that they are also vulnerable to all sorts of pollution, the evidence is weak (Bourne 1976). There is at present anxiety about the effect of some fishing methods, such as long-lining, which may be endangering species such as the great albatrosses.

All species feed at sea on a variety of fish, cephalopods and small marine invertebrates, either socially or alone; larger species may scavenge all sorts of offal or prey on other birds. Most, except perhaps *Pelecanoides*, can digest the complex lipids formed by some marine animals (Clarke & Prince 1976), and may eject them to soil the plumage of their enemies with lethal results (Swennen 1974). Some species can digest wax (Obst 1986). Many now take wastes from whaling and fishing operations (Fisher 1952). All have long life-cycles in proportion to their size; they disperse on fledging and then prospect for nest-sites for 2–12 years in their youth. They usually lay a single large white egg annually; though a successful breeding cycle may be completed in less than a year in at least one tropical species, *Puffinus lherminieri*, it may take 2 years in larger southern ones. Before laying, the birds court for weeks or months, then go to sea for feeding. Incubation lasts 6–8 weeks, and fledging 2–9 months. Once the fat chick fledges it fends for itself, even in species that immediately make a long migration, sometimes to the opposite hemisphere.

Tendency for failed breeders and non-breeders to begin moult before successful breeders. Five strategies of wing-moult in breeding adults: (1) In albatrosses, remiges replaced in staffelmauser interrupted while breeding; in nearly all other species, primaries moulted outwards; possibly simultaneously in some diving-petrels. (2) In most subantarctic and temperate species, moult begins soon after breeding and is completed shortly before next breeding season. (3) In most tropical species, moult aseasonal, between breeding attempts; resumption of breeding apparently depends on when moult completed. (4) In trans-equatorial migrants, wing-moult delayed until they reach non-breeding quarters, where it is completed; moult rapid but no satisfactory evidence for flightlessness. In

263

264 Diomedeidae

some species, body-moult also in winter quarters; in others, at breeding grounds. (5) In some species of high latitudes, rapid moult completed in summer when they breed; some begin moult long before breeding finished.

The history of the classification of the Order is very confused, as is seen by comparing Timmermann's (1965) discussion of their Mallophagan parasites with that by Klemm (1969) of their leg muscles and that by Harper (1978) of their proteins, but it is now widely agreed that the Order is best divided into four families: Diomedeidae or large to huge aerial albatrosses; Procellariidae or medium-sized, mainly aerial but sometimes aquatic, petrels, shearwaters and prions; Hydrobatidae or small to tiny, aerial storm-petrels; and Pelecanoididae or small aquatic diving-petrels.

References

Bang, B.G. 1966. Acta anat. 65: 305-415.
Bourne, W.R.P. 1976. Pp 403-502. In: Johnston 1976.
Brodkorb, P. 1963. Bull. Flor. St. Mus. biol. Sci. 7: 179-293.
Clarke, A., & P.A. Prince. 1976. J. Exp. mar. Biol. Ecol. 23: 15-30.
Fisher, J. 1952. The Fulmar.

Harper, P.C. 1978. NZ J. Zool. 5: 509-549.

Johnston, R. (Ed.). 1976. Marine Pollution.
Klemm, R.D. 1969. S. Ill. Univ. Monogr. Sci. Ser. 2.
Obst, B.S. 1986. Wilson Bull. 98: 189–95.
Olson, S.L. 1975. Smithson. Contr. Paleobiol. 23.
Swennen, C. 1974. Ardea 62: 111–117.
Timmermann, G. 1965. Abh. Verh. naturwiss. Vereins Hamburg NF 8, Suppl. 1–249.

aterally compressed with legs set far back in aquatic ones. The front toes are webbed; hind toe small or absent The proventriculus is long and glandulär; the gizzard small and twisted; and the small intestine often spiral in

Family PROCELLARIIDAE fulmars, petrels, prions, shearwaters

The family Procellariidae represents the main radiation of medium-sized 'true petrels', characterized by having united nostrils with a median septum and the outer functional primary at least as long as the next. It tends to be dominant among the birds of the Southern Ocean, though in the n. hemisphere the Charadriiformes are more numerous. The giant-petrels *Macronectes* have also developed as large scavengers and predators, showing some convergence in appearance and behaviour with the Diomedeidae. The Procellariidae may be divided into four main groups with some intermediate species, which makes it hard to draw distinctions between them.

(1) The fulmars Macronectes, Fulmarus, Thalassoica, Daption and Pagodroma consist of seven species of surface predators and filter-feeders of rather varying structure and appearance (Voous 1949) that breed in high latitudes but may migrate along cool currents into much lower ones. Fulmarus appears to have colonized the n. hemisphere in the Tertiary. Six of the seven species are essentially confined to our region.

(2) The gadfly-petrels *Pterodroma* are a large series of some 30 agile species; 16 breed in our region and another six occur rarely or rather rarely. Their short sturdy bills are adapted for seizing soft prey at the surface, and their twisted intestines, for digesting marine animals with an unusual biochemistry, which are also found throughout the warmer oceans (Imber 1985). They show complex markings of face and wings that must serve as interspecific recognition-marks (Murphy & Pennoyer 1952). Some species placed in this group have an intermediate structure and intergrade with all other groups distinguished here: *Pterodroma* (*Lugensa*) brevirostris, which moves S in winter, has distinctly big eyes like *Pagodroma*; *Halobaena caerulea* has a plumage similar to that of prions; *Bulweria* has some structural resemblance to shearwaters. At present it is difficult to determine their precise relation-ships.

(3) The prions *Pachyptila* are a specialized group of six (perhaps five) very numerous species, all in our region, that show a progressive adaptation of a small, agile, cryptically coloured, fulmarine form for filter-feeding on zooplankton. There has been dispute over their classification (Cox 1980; Harper 1980) but the arrangement discussed by Fleming (1941) seems best except that the Broad-billed Prion *P. vittata* appears to intergrade with Salvin's Prion *P. salvini* through *macgillivrayi* of Ile St Paul; so they may be better treated as subspecies of the same species.

(4) The shearwaters *Procellaria*, *Calonectris* and *Puffinus* include some 20 agile species with long bills adapted to catch prey more or less under water throughout the warmer seas (Kuroda 1954); 13 species breed in our region, some migrating into the n. hemisphere; six others are chance or perhaps regular visitors. From the fossil record (Brodkorb 1963; Olson 1975); they seem to have been particularly common in the great Tethys Ocean of the middle latitudes of the n. hemisphere in the Tertiary, so this development of aquatic habits may have occurred there without competition from penguins with a subsequent return S by the more successful forms.

General features of the family are: body, ovate, or elongate in shearwaters; wings, long and narrow, 11 primaries, p10 longest, p11 minute; 20–29 secondaries, short, diastataxic; tail, short, 12 feathers; bill, heavy (*Macronectes*), slender (shearwaters), broad (prions) or stubby (gadfly-petrels), hooked, formed of several horny plates; nostrils in dorsal tube of varying length; legs set far back, laterally flattened but round in gadfly-petrels; three toes, webbed, hind toe vestigial, raised. Oil-gland feathered. Peculiar musky odour. Sexes similar, male usually larger than female. Plumage, black or grey above, white below, or all dark; light and dark morphs in some species. Juveniles and immatures usually like adults.

Cosmopolitan throughout the oceans, essentially pelagic; more abundant in cool or cold waters rich in plankton and mostly away from ice. Swim well but usually aerial except when feeding or resting. Fly with alternate swooping and flapping action close to the surface but often arcing high in some gadfly-petrels. Gait on land, a shuffling crouch, being unable to walk properly with feet set so far back; generally avoid open areas on land, being thus vulnerable to predators. Nest colonially; for the most part in burrows and cavities in all sorts of terrain, sometimes far from the sea and in mountainous areas but some species, e.g. *Macronectes*, nest on open ground. Hole-nesters usually nocturnal at colonies, when often extremely vocal, though generally silent at sea. Migratory and dispersive. Some species divide the year between s. and n. hemisphere, often migrating in large flocks that may settle on the sea in huge dense rafts. Feed mostly on fish, cephalopods and crustaceans obtained by flight-feeding, plunge-diving, surface feeding, surface-diving and underwater pursuit; hydroplaning (Murphy) is a characteristic method used particularly by prions.

Probably all defend small nesting territories to which they return regularly while undisturbed; certainly so in some hole- and burrow-nesting forms. Agonistic and sexual behaviour of nocturnal, hole-nesting species very poorly known but generally seem to have little specialization for visual displays. Tactile actions such as allopreening and billing used but olfactory and vocal communication is probably important. Breeding is usually seasonal, generally with synchronized laying, often after a pre-laying exodus but some may not nest annually; some have shorter

356 Procellariidae

cycles or nest continually. For the most part, little attempt to make substantial nests. Eggs, ovate, mat, white. Clutch-size, invariably one; single-brooded; no replacement laying. Incubation by both sexes in alternate spells of 1–11 days. Single median brood-patch. Incubation period, 45–55 days. Eggshells probably always trampled in nest. Young, semi-altricial, nidicolous; hatched in down. Rarely left alone in nest for first 1–2 weeks. Cared for and fed by incomplete regurgitation by both parents. Nestling period generally shorter in cliff- and ledge-nesting species than in hole-nesters. Young attain greatest weight, often well above that of adult, some days before fledging, by which time weight has been reduced to about the same as an adult, but no clear evidence that young are totally deserted for last few days in nest. Adults and young of most species liable to eject stomach-oil in defence. Young independent at fledging. Maturity reached at minimum of 3–4 years, in some 6–12 years.

REFERENCES

Brodkorb, P. 1963. Bull. Flor. St. Mus. biol. Sci. 7: 179-293.
Cox, J.B. 1980. Rec. S. Aust. Mus. 10: 91-121.
Fleming, C.A. 1941. Emu 41: 134-55.
Harper, P.C. 1980. Notornis 27: 235-86.
Imber, M.J. 1985. Ibis 127: 197-229.
Kuroda, N. 1954. On the classification and phylogeny of the order Tubinares, particularly the shearwaters (Puffinus),

with special consideration on their osteology and habit differentiation. Tokyo.

Murphy, R.C., & J.M. Pennoyer. 1952. Am. Mus. Novit. 1580.

Olson, S.L. 1975. Smithson. Contr. Paleobiol. 23. Voous, K.H. 1949. Ardea 37: 113-22.

Pagodroma nivea Snow Petrel

Procellaria nivea Forster, 1777, Voy. Wld 1: 96, 98 - lat. 52°S, long. 20°E.

Generic name compounded of Greek $\pi \dot{\alpha} \gamma \circ \zeta$ (ice) and $\delta \rho \dot{\omega} \circ \zeta$ (race, running); specifically, the Latin *niveus*, snowy; thus, the snowy ice-runner.

OTHER ENGLISH NAMES Snowy Petrel.

POLYTYPIC Nominate nivea breeds Antarctic continent and Peninsula, S. Georgia, islands of Scotia Arc; confusa Mathews, 1912, breeds Pointe Géologie Arch., Terre Adèlie, Balleny Is, Peterson Is, Ardery I., Proclamation I., S. Sandwich Is, C. Hallett and C. Hunter.

FIELD IDENTIFICATION Length 30–40 cm; wingspan 75–95 cm; weight 240–460 g. Smallish, lightly built petrel; the only small all-white petrel. Black bill, eyes and feet provide striking contrast to white plumage. Sexes alike. No seasonal changes. Juveniles inseparable.

DESCRIPTION ADULT. Plumage entirely white with subtle ivory tone, contrasting with black bill and feet and conspicuous dark eyes. Some birds (possibly immatures) have shadowy markings on back and upperwings, and grey wash or fine speckling on tips of remiges. Bill, short and blue-black. Iris, very dark brown. Legs and feet, blue-black.

SIMILAR SPECIES No other small all-white petrels, though albino forms of shearwaters and other petrels, away from pack-ice, might be confused. Other mainly white birds in Antarctic seas are Arctic Sterna paradisaea and Antarctic S. vittata Terns and white morph of Southern Giant Petrel Macronectes giganteus, but all easily distinguished.

Range restricted to pack-ice and adjacent Antarctic seas. Flight erratic and buoyant; frequently change direction; fly with rapid shallow wing-beats and infrequent glides. Fly easily in blizzards and strong winds with wings held close to body. Appear long winged in flight with nearly square tail when folded but distinctly wedge-shaped when fanned. At distance in poor light, may appear pale grey. Hover low over water but rarely seen swimming. Do not normally follow ships but often circle slow moving ships in pack-ice. Flocks often roost on icebergs.

HABITAT Circumpolar in Antarctic waters, from limit of pack-ice in N to continental ice-shelf in S. Strongly associated with pack-ice, to which may be restricted by flight

characteristics unsuited to pelagic journeys (Griffiths 1983). In Ross Sea, highest densities in belt overlying continental slope (Ainley et al. 1984). Seldom in waters N of pack-ice, but occasionally concentrate in open water where icebergs present (Routh 1949; Ainley et al. 1984), or at sources of abundant food (Falla 1937), especially over continental slope in w. Ross Sea (Ainley et al. 1984). Occur far from pack only near icecovered islands e.g. S. Georgia, Scott I.; where observed around drifting ice offshore and at heads of glaciers (Murphy); may be closely associated with icebergs at these localities or may cross large tracts of open water to edge of pack-ice for feeding (Ainley et al. 1984). Three vagrants seen at Heard I. when sea surface-temperature -0.22 °C and pack-ice within 300-400 km of island (Gilchrist 1952). Observed in Antarctic inland in breeding season; in non-breeding season, dispersed at sea beyond zone of fast-ice (Johnstone et al. 1973), but approach coast if strong winds break up sea-ice (Cowan 1979). Highest densities within 350 km of known nesting areas (Ainley et al. 1984).

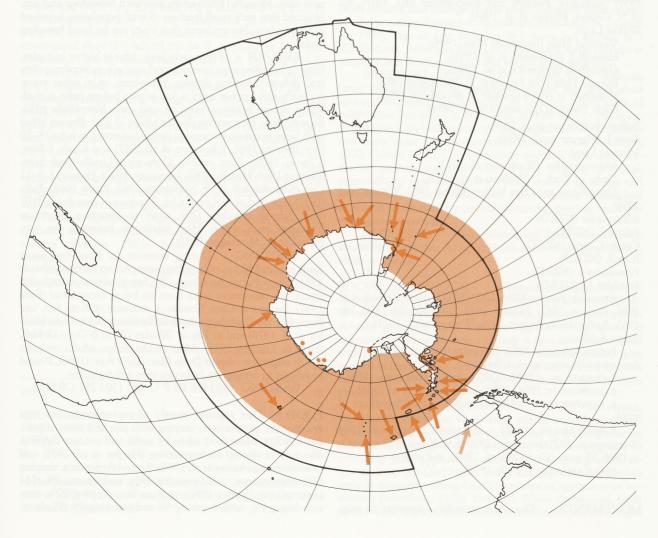
Within pack, highest densities along ice edge; less common in interior (Routh 1949; Ainley *et al.* 1984; Montague 1988). Prefer light pack-ice; 10–30% ice-cover (Weddell Sea; Cline *et al.* 1969); 12–50% (Ross I. to Anvers I.; Zink 1981); <62% (Ross Sea; Ainley *et al.* 1984); 0–25% (Prydz Bay; Montague 1988). At C. Crozier, occurrence related to ice cover and wind speed and direction. When pack-ice present, number/h observed inversely related to ice-cover; rare when pack-ice absent or when heavy and unbroken. Numbers increase as strength of s. offshore winds increases above 38 km/h; perhaps because s. winds blow pack offshore and decrease ice-cover (Ainley *et al.* 1978). Within pack-ice of Ross

Sea, 65% total observations at leading edge of floes; 22% over brash-ice; 12% over leads; 1% over floes (Ainley *et al.* 1984). Feed near icebergs, among ice fragments at base or in leads opened by drift (Falla 1937; Routh 1949). At Heard I., vagrant birds fed beyond breakers in backwash extending into bay (Gilchrist 1952).

Breed S of Antarctic Convergence, on islands and on Antarctic continent, from coast to up to 300 km inland (Lovenskiold 1960; Van Autenboer 1962; Brown 1966), Nest in steep rocky situations with nesting cavities; on fissured rock of cliffs, mountain peaks, ridges; or on higher levels of moraines where wind removes all but the larger rocks, and nest cavities plentiful (Brown 1966). Breeding distribution determined by presence of residual pack-ice, and colonies far from pack are small (Ainley et al. 1984). Within these limits, choose nesting areas where snow does not accumulate, blocking nest entrances; sites therefore often high and exposed, or oriented towards prevailing wind (Johnstone et al. 1973; Cowan 1981; Brown 1966); lower sites on coastal cliffs often on leeward side, where crevices less readily blocked by frozen spray (Brown 1966). On coast, nest from close to water's edge up to 370 m asl (Maher 1962); in inland mountain ranges, up to 2400 m asl (Bowra et al. 1966).

Rest on icebergs and floes (Routh 1949; Harper 1987). When foraging, fly low over water, obtaining food on or just below surface (Zink 1981; Harper 1987). Direct flight over ice or water at 7–10 m (Zink 1981); soar near colonies to 900 m; at Mawson, recorded flying inland at heights of up to 1800 m (Brown 1966).

DISTRIBUTION AND POPULATION Confined to Antarctica; distribution highly correlated with density of pack-ice, rarely more than few kilometres from it except near breeding colonies lying to N of limits of pack-ice (Bouvetøya, S. Georgia); roughly within limits of five-tenths ice-cover (Griffiths 1983). Reach farthest N in Sept.-Oct.; about 50°S in Atlantic, Indian Oceans (Watson et al. 1971); about 55°S in Aust. and Pacific sectors (Watson et al. 1971; Szijj 1967). In Feb.-Mar., confined to narrow zone round Antarctic continent or may disperse; but less common round w. Antarctica where heavy pack ice persists most years. More common at S. Orkneys than at S. Shetlands, probably because of different ice-conditions, though latter farther S (Bennett 1920). Probably has never occurred in Aust. waters. Skin in MV labelled 'S seas off A', but HASB rightly dismisses it as unlikely to have been collected near the continent. Two sightings claimed: off Newland Head, SA, 15 Sept. 1974 (Cox 1976); in Port Phillip Bay, Vic., 6 Oct. 1974 (Hyett 1974); inadequately authenticated and not accepted. Recorded in Falkland Is (Wace 1921; Watson et al. 1971); unknown from S. Africa with nearest



record at 52°S, 20°E (Murphy); apparently not recorded from S. America. No recent records NZ (NZ Atlas).

S. limit on coast of Antarctica, fast-ice or very heavy pack-ice without leads or pools of water (Watson *et al.* 1971; data from Armstrong *et al.* 1973; Antarctic Pilot 1974). In summer may wander 100 km inland, even into areas far from breeding colonies (Wilson 1907; Falla 1937). Occasional to Heard I. (Gilchrist 1952) and Iles Kerguelen (Derenne *et al.* 1974).

BREEDING Wherever exposed rock in summer, under overhangs or in small caves; generally on coast of Antarctic continent and Pen. except e. coast of Pen. or w. Antarctica, which are enclosed by extensive heavy ice in all seasons; also on glaciated islands S of Antarctic Convergence. Locations listed below (from Watson *et al.* 1971 unless stated); on inland mountain ranges to 400 km from open sea; most southerly: Mount Faraway, Theron Mts (Brook & Beck 1972).

ANTARCTIC CONTINENT

Dronning Maud Land (Lovenskiold 1960; Ryan & Watkins 1988): Muhlig-Hofmann, Wohlthat and Sor-Rondane Mts (A.N. Cowan);

Mac.Robertson Land: Scullin Monolith; Reeves Hill, Casey, Ardery and Peterson Is (T.A. Montague);

Edward VII Land and Marie Byrd Land (Siple & Lindsey 1937): Saunders, Fosdick and Rockefeller Mts, Perry Ra. (A.N. Cowan; Harper *et al.* 1984);

Wilkes Land:

Vestfold Hills (Jouventin et al. 1984). Haswell I. (Jouventin et al. 1984). Gaussberg (Jouventin et al. 1984). Bunger Hills (van Franeker & Montague 1987). Windmill Is (van Franeker & Montague 1987). Cape Denison (Jouventin et al. 1984).

Balleny Is (Harper et al. 1984).

Scott I. (Harper et al. 1984).

Victoria Land:

Morozumi Ra. (Watson et al. 1971).

Duke of York I. (Watson et al. 1971).

Cape Adare and Cape Hallett (Maher 1962; Watson *et al.* 1971).

Edisto Inlet (NZRD).

Felsite I. (NZRD).

Crater Cirque (NZRD).

Ross I. (NZRD).

Possession I. (NZRD).

Franklin Is. (NZRD).

Antarctic Pen.: <1984: 1000-10 000 pairs (Croxall et al. 1984; Perkins 1945; Eklund 1945; Lovenskiold 1960; Loy 1962; Ardus 1964; Brown 1966; Watson et al. 1971). Terre Adèlie

Pointe Géologie 1963: 500 pairs (Prévost 1963). Bouvetøya (Harper *et al.* 1984).

S. ORKNEY IS: <1984: 1000 pairs (Croxall et al. 1984).

s. GEORGIA: <1984: 3000 pairs (Croxall et al. 1984).

s. SANDWICH IS: <1984: c. 1000 pairs (Croxall et al. 1984).

s. SHETLAND IS: <1984: c. 100 pairs (Croxall et al. 1984; Watson et al. 1971; Isenmann 1970; F.C. Kinsky); Elephant I.: <1984: 55 pairs (Croxall et al. 1984); and others.

PROCLAMATION I. (Falla 1937).

MOVEMENTS I

Dispersive, possibly migratory to edge

of pack ice during winter when sea near breeding sites frozen.

DEPARTURE Adults leave Haswell I. late Apr.mid May (Nudelman 1962; Pryor 1968), Davis 25 May-5 June (Brown 1966; Johnstone *et al.* 1973) as sea starts to freeze (Brown 1966) with numbers declining at other breeding colonies from Mar. (Signy I.; Rootes 1988). Young fledge late Feb.-early Mar. at Davis (Brown 1966; Johnstone *et al.* 1973) and Signy I. (Beck 1970); at Dumont d'Urville 24 Feb.-17 Mar. (Mougin 1968; Isenmann 1970).

NON-BREEDING Winter movements little known. In some areas may be rather local, birds being present entire year, especially where pack-ice shifts continually (Clarke 1906; Gain 1914; Dupond 1946; Johnstone et al. 1973; Rootes 1988). At other Antarctic stations winter records irregular, chiefly during mild weather or when wind and tide produce open pack-ice near shore (Eklund 1945: Prévost 1964; Mougin 1968); large numbers seen near Palmer Stn late Apr.-June but not later in winter (Parmelee et al. 1977), and large numbers visit colonies in Adèlie Land in May (P. Jouventin). Numbers seen during winter higher at lower latitudes but vary between years (Falla 1937; Eklund 1945; Gilchrist 1952; Prévost 1964; Brown 1966; Mougin 1968). Snow Petrels visiting land during winter may alight on cliffs in large numbers (Rymill 1938) and Brown (1966) reported them sitting on nest-sites. Mougin (1968) never saw such behaviour and emphasized that only small fraction of total population involved in these visits. No evidence that visits are by local breeding birds.

RETURN From early Sept., later at higher latitudes. visits to breeding sites intensify and may merge imperceptibly into definite breeding activity. Elsewhere, or in other years, no birds may appear until a few weeks before main arrival, which occurs between late Oct. and early Nov. (Falla 1937; Brown 1966). First arrives Davis 13 Sept.-1 Oct. (Brown 1966) with large numbers occupying nesting sites at Davis by 18-20 Oct. (Brown 1966; Johnstone et al. 1973) and Casey 1 Nov. (Cowan 1979). First arrivals Dumont d'Urville mid Sept. (Prévost 1964; Mougin 1968; Isenmann 1970), Haswell I. 5-31 Oct. (Korotkevich 1959; Nudelman 1962; Pryor 1968). Falla (1937) reported arrival on 6 Oct. Thousands seen flying NW over Palmer Stn late Oct. were in breeding condition (Parmelee et al. 1977). High fidelity to breeding site (van Franeker & Montague 1987).

BREEDING During summer in Ross Sea, most birds within 550 km of breeding sites (Ainley & Boekelheide 1983). Snow Petrels breeding at S. Georgia are associated with glacial ice, movement away from ice being exceptional (Falla 1937). Present at Cape Crozier, s. extreme of Ross Sea, late Nov.-late Dec., when pack-ice still present but broken (Ainley *et al.* 1978) and at Bay of Whales (78°S) 6 Oct.-13 Mar. (Siple & Lindsey 1937). After chicks fledge, adults undergo moult migration; absent Davis Mar.-early Apr. (1966). Found beachcast in temperate latitudes very infrequently.

BANDING. 66S140E 02 P U 182 1303 257 CRBPO

FOOD Diet consists mostly of cephalopods, fish and crustaceans, proportions varying with site and time of year. BEHAVIOUR. Most food taken by aerial-and contact-dipping, also surface-diving, surface-seizing (Harper *et al.* 1985) and pursuit-diving (Ainley *et al.* 1984). Round Antarctica, dipping 66% observations, surface-seizing 25%, ice-gleaning 9% (214 observations; Harper 1987); in Ross Sea, dipping 90%, pursuit-diving 4%, surface-seizing 4% and pattering 2% (55 obser-

vations; Ainley et al. 1984); Griffiths (1982) observed only dipping, Gilchrist (1952) surface-seizing. Feed in open leads among floes with gliding and skimming flight, sometimes hovering kestrel-like above water before swooping quickly down to surface (Harper 1987). Also hover low over edges of floes to pick up food thrown up by surf (Wilson 1907) or trapped by freezing on upturned surface (Harper 1987; Murphy). In wind, patter on lee side of icebergs, head to wind, wings raised, feet treading water (Falla 1937). Sometimes pursuit-plunge into water with open wings, submerge completely and return to surface with wings still open (Gain 1914). When surfaceseizing, may peck continuously while rotating body with feet (Gilchrist 1952). Detection of food partly by scent (Jouventin 1977); flight paths deviated towards sponge soaked with cod liver oil but not to one soaked with mineral oil (Jouventin & Robin 1984); but can find nesting sites by sight alone (Haftorn et al. 1988). Will feed in association with Minke Whales Balaenoptera acutorostrata (Griffiths 1983; Enticott 1986) and Antarctic Petrels Thalassoica antarctica (Griffiths 1982; Harper 1987).

NON-BREEDING At deep-ocean localities in Ross Sea (three stomachs; Ainley et al. 1984) cephalopods Psychroteuthis glacialis 65.6% wt., 5.0% no., 33% freq., crustaceans euphausiids Euphausia superba 34.4, 95, 100, 4.0 cm (0.5; 12); over continental slope (30) cephalopods 63.2% wt. Gonatus antarcticus 0.8% no., 10% freq., 66 g (8.0), 14.0 cm (6.0; 4), Psychroteuthis glacialis 1.6, 10; crustaceans 36.8 (E. superba 95.3, 93, 3.7 cm (0.3; 112)); unident. Lysianasiidae 1.6, 10; over continental shelf (21) fish 90.6% wt. (Lampanyctus 2.7% no... 14% freq., Pleuragramma antarcticum 83.8, 14, 11.2 g (3.2), 12.2 cm (3.5; 94)), cephalopods 8.3 (P. glacialis 2.7, 14; unident. 5, 2.7), euphausiids 1.1 (E. crystallorophias 8.1, 14, 2.1 cm (0.4; 9)). In e. Weddell and s. Scotia seas (17; Bierman & Voous 1950), fish 89% freq., cephalopods 67, crustaceans 61, gastropods 11; in s. Indian Ocean (17; Falla 1937) crustaceans 88% freq. (Euphausia 71, pelagic prawns 12), fish 12, cephalopods 35, pteropods 12, and offal 6; in Southern Ocean (22; Griffiths 1983), crustaceans 73, fish 55, cephalopods 86. Also recorded taking small silvery fish (Eklund 1945), one bird disgorging 40-50; isopod Anurops antarcticus (Hale 1952). Many authors have described opportunistic feeding on galley scraps, seal carcasses (Griffiths 1983), whale blubber, seal placentae, carcasses of other seabirds including other Snow Petrels, and excreta (Prévost 1953; Brown 1966; Watson 1975; Murphy).

BREEDING Summarized Table 1. At Terre Adélie, fish 95% wt., 64% no., 50–120 mm; crustaceans euphausiids 2,

Table 1. Frequency (%) of food types in diet of breeding Snow Petrel.

	1	2	3	4	5
FISH	13	di tetih	60	31	10
CRUSTACEANS CEPHALOPODS	25	100	40	15 23	
OFFAL	69			≥ 23	11
n	16	?	5	13	26

(1) Ile Petermann (Gain 1914). (2) Davis (Brown 1966). (3) Cape Hallett (Maher 1962). (4) Terre Adélie (Mougin 1968, 1975). (5) Terre Adélie (Ridoux & Offredo 1989). 24, 42% freq. (Euphausia crystallorophias, E. superba), amphipods Hyperiidae -, 1, 11 (Themisto gaudichaudii), Gammaridea -, 8, 35, 10–33 mm; cephalopods 2, 2; carrion 1, 1 (Ridoux & Offredo 1989); at same site feathers of Adélie Penguin Pygoscelis adeliae 23% freq., seal placenta 8 (Mougin 1968, 1975); at Ile Petermann offal from seals (Gain 1914); at Davis crustaceans all Euphausia superba 1–2.5 cm (Brown 1966).

INTAKE Feeding frequency at Terre Adélie 0.51 meals/day (72; Ridoux & Offredo 1989).

SOCIAL ORGANIZATION Information supplied by A.N. Cowan. Loosely gregarious at sea and when breeding. Large numbers together at sea when attracted to food but often seen singly. Flocks do not show co-ordinated flying movements as in Antarctic Petrel but individuals fly about in 'mazy fashion' (Wilson 1907). Often associate with Antarctic Petrels. When breeding and to some extent at sea, nocturnal, thus resembling Wilson's Storm-Petrel and not other fulmarine petrels. Little information on behaviour at sea and in pack-ice from lack of opportunities for observing.

BONDS Monogamous. Pair-bonds last long (Brown 1966; Guillotin & Jouventin 1980); 30% of pairs stayed together for 4 years (Mougin 1975); annual rate of divorce 17%. Show strong fidelity to nest-site; 37% of birds stayed at same site for 6 years (Mougin 1975); change of site, 13% per annum. Both divorce and change of site more common after unsuccessful breeding during previous season (Guillotin & Jouventin 1980). Age at first breeding 6-7 years but known at 5 (Guillotin & Jouventin 1980); pair-formation starts perhaps at younger age. Both parents tend young until fledging.

BREEDING DISPERSION Not truly colonial; large concentrations in favourable habitat but nests often sparsely scattered. Nests usually in crevices out of sight of neighbours but when in open sites, may be only 1–2 m apart, outside pecking but within spitting distance. Sometimes several nests close together in caves (Clarke 1906; Isenmann 1970; Cowan 1981). Often associate amicably with other fulmarine petrels, especially Cape Petrel. Highly territorial, essentially in nest-site territory only, consisting of site and surrounding rocks to distance of 1 m, including landing and approach route; used for courtship, mating, nesting, rearing of young and roosting.

ROOSTING Before laying and during breeding season only at nest-site. At other times on icebergs, snow-banks, often in flocks.

SOCIAL BEHAVIOUR Information supplied by A.N. Cowan. Partial studies by Isenmann (1970) and Brown (1966). When at sea, apparently little communication between individuals; generally silent and not aggressive. On arrival at colonies, spend much time roosting at nest sites, interrupted with periods at sea; become more active in late afternoon with periods of flight round cliffs from dusk to early morning; birds stained with oil from fighting gather on snow-banks to clean plumage.

AGONISTIC BEHAVIOUR Early in season, mated pairs sitting on rocks near site or outside nests call loudly at intruders flying low overhead or landing nearby; male attacks and spits oil at intruders. Male seeking nest or intruding male approaches silently, evoking aggressive response from installed birds; female seeking mate approaches male at nest-site, calling loudly, perhaps as appeasement behaviour (Isenmann 1970). THREAT. When threatened, birds stretch neck slightly, lower head, screech and eject oil to repel intruders. When approached on nest, sitting bird does not call or move until observer within 1-2 m (range of spitting); then spits repeatedly; seizes outstretched hand with harsh calls, still extruding oil through nostrils. FIGHTING. Fights start if threats not effective; intruders may be unmated males approaching mated pair or another mated pair attempting to enter nest-site. Male rushes at intruder at nest entrance; birds grasp each other's bills and violently lever heads, screech, beat wings and regurgitate oil; males roll over and over using wings for balance and leverage. Females may screech and peck indiscriminately at both contestants. Bird holding lower mandible usually wins. Losing bird flies off, often being chased into air by victor. Leads to Aerial Fight: common; involves complex manoeuvres and shrill chattering, birds sometimes locking bills and tumbling in the air (A.N. Cowan); described by Brown (1966). Victor pursues loser into air, grasping tail feathers in flight; sometimes pulls one or two feathers out. Occasionally grasps flank of losing bird; both birds fall to ground and then resume fight. Fights may last 1-2 h and birds may be injured. Unpaired birds may continue to harass and challenge paired birds till mid-Dec. Birds in possession of site appear to have advantage; in 20+ fights observed, intruder always lost (Brown 1966). P. Jouventin suggests that Aerial Display flight (see Courtship) is an agonistic behaviour.

SEXUAL BEHAVIOUR Early arrivals often sit quietly on ledges but do not occupy nest-sites until snow melts and main influx of birds occurs (Brown 1966). ADVER-TISING. While females sit in front of nest-site or on prominent rocks, males perform Aerial Flights: male flies back and forth over nesting area, eventually making hesitant close approaches to female; in response, she calls and shuffles about with bill wide open and head upturned towards flying male. This display appears to be invitation to COURTSHIP; mutual acceptance followed by Aerial Display Flight: female flies along cliff c. 15 m asl at normal flight speed, male following about 1 m behind. After about 10 s, both birds slow and female begins chirring continuously; male immediately responds with Main Call. While calling, birds perform semigliding, fluttering flight for c. 10 s, male very close to female: wings held high, feet held down, bodies arched, and head and tail pointed up. Birds then drop down together, before resuming normal flight and calls, and returning to nest (Brown 1966). This display often followed by allopreening at nest, calling and quick touching and retraction of bills. Displays occur until early Dec. (Falla 1937); peaks first or second week Nov. and repeated several times each evening till copulation takes place (Brown 1966); after copulation mated birds rarely display (Brown 1966). Aerial Chases. Non-breeders continue to display till late-Nov. but females respond only weakly, if at all, to following males and by Dec. displays become chases with female taking refuge on ground. GREETING CEREMONY simple; incoming bird circles nest-site several times before alighting; birds call (see Voice), facing each other with necks outstretched. Relieving bird sits 10-15 cm from mate, which then stands and moves away from egg; relieving bird moves to egg, stands over it and tucks it under body with bill. Birds Cluck softly until relieving bird settled, then call together; occasionally mutual preening between calls. Relieved bird always circles nest several times before departing. Departure immediately after nest-relief or up to a few hours later (Brown 1966). Visits to nest between change-overs rare. ALLOPREEN-ING. Birds allopreen and nibble head, nape and bill of mate. COPULATION. Occurs mostly in early (5-15) Nov., usually (A.N. Cowan) or always (Brown 1966) at night and outside nest (Brown 1966). At dusk, birds sit together at nest entrance, calling frequently, rubbing bills and mutual preening. Female often places bill in bill of calling male; male responds by pressing underside of bill on female's forehead and nape. Female spreads wings slightly and male stands on back, shifting weight from one foot to the other and rubbing female's bill and forehead. This continues for several minutes and intensifies, birds calling throughout; male gives series of soft clucking calls, female high-pitched chirring. Male then moves one foot to upper tail-coverts of female, who moves tail to one side; male lowers his tail to make cloacal contact. After copulation. male usually slides to rear and sits motionless while female preens; then birds make short flight. Pairs may copulate once only after many unsuccessful attempts. If female unwilling, she pecks male and screeches. Both birds often fly away after the event. Birds clear nest-site before pre-laying exodus, during this period making frequent short flights from nest.

RELATIONS WITHIN FAMILY GROUP No detailed knowledge. Parents brood chicks alternately and continuously for varying periods (see Breeding). When being fed, chick rubs bill on adult's bill and *chirrups*; then places bill inside adult's during regurgitation; preens after being fed. Adults recognize site, not chick, and accept exchanges (Isenmann 1970).

VOICE Only detailed study that of Guillotin & Jouventin (1980); behaviour, including descriptions of calls, studied by Brown (1966). Usually silent at sea but may twitter like European Linnet Carduelis cannabina (Lowe & Kinnear 1930). Harsh guttural calls at breeding sites; may be heard to 1 km; from late-Oct. to late-Feb. or early Mar. Limited range of calls; most based on series of harsh staccato notes described as high-pitched ke-ke-ke (Eklund 1945) or hoarse kir-kir-kir (Bierman & Voous 1950); also chirring, clucks and screeches. Calling associated with agonistic interactions and aerial displays mostly early in breeding season, continuing to early or mid-Dec. Pairs duet, using same call (Brown 1966; Guillotin & Jouventin 1980). Distinct sexual differences in calls (Isenmann 1970; Guillotin & Jouventin 1980); fundamental frequency of male's song invariably lower than female's; respectively 2.46 kHz (2.2-2.8; 8), and 3.43 kHz (2.7-4.0; 6). Fundamental frequency inversely correlated with weight of birds; male generally heavier than mate (Guillotin & Jouventin 1980) and calls of males generally pitched lower than those of females (Brown 1966; Guillotin & Jouventin 1980); pitch falls as weight of individual rises, more evidently among females than males. No geographical variation indicated; calls from Dumont d'Urville indistinguishable from those at S. Orkneys (Guillotin & Jouventin 1980).

ADULT (1) Main call (Defence Call): series of harsh staccato notes described as five or six rough guttural caws k-k-k-kaa-kaa-kaa-kaa-kaa; begins softly and lowpitched, reaching greatest volume and highest pitch at first or second kaa; remaining notes longer and descending scale (Brown 1966); lasts 4 (Guillotin & Jouventin 1980) to 10 s (Brown 1966). Also described as high-pitched ke-ke-ke (Eklund 1945); hoarse kir-kir (Bierman & Voous 1950); probably equivalent to guttural and disagreeable teck-teck-teck (Watson 1975); rasping cluck (Eklund 1945) or harsh chatter (Ardley 1936). Sexual differences described above. Given by both sexes during Courtship Displays, Mutual Aerial Display, at nest (sonagram A) and in response to intruders and when approaching nest at change-over or for feeding chick. Calls of



K. Green, ANARE; Rauer Is, E. Antarctica, Dec. 1984-Jan. A 1985: B910

parent when approaching to feed chick probably inhibit spitting by chick (Isenmann 1970). (2) Chirr. Given during Mutual Aerial Display by both sexes (Brown 1966); perhaps agonistic call (P. Jouventin). Female gives high-pitched chirr during copulation. (3) Cluck. During copulation, male gives soft clucks (Brown 1966); both sexes cluck between regurgitations when feeding young. (4) Screech. Given by both sexes during Fights. Other Calls. Whine (Pryor 1968) or plaintive cry (Prévost 1953) reported during copulation. When spitting at intruder, regular mechanical hic-hic is given.

Chirrup continuously when parent enters YOUNG nest; ceases when adult departs (Brown 1966).

BREEDING Fairly well known. Detailed studies at Dumont d'Urville (Mougin 1968, 1975; Isenmann 1970); at Mawson and near Davis (Brown 1966). Information supplied by A.N. Cowan. Breed in simple pairs, colonially, often in company with Southern Fulmars, Antarctic and Cape Petrels.

SEASON Late Nov. to mid-Mar.; no variation on Continent, coastal or inland; possibly a few days earlier in S. Orkneys (Clarke 1906). Unexpectedly early hatching, one month before normal, at Tottanfjella (74°S, 12°W; Bowra et al. 1966), perhaps in abnormally warm season; not confirmed by Lovenskiold (1960), Loy (1962) or Ardus (1964). Arrival at colonies synchronized in Oct.-early Nov.; on Palmer Pen., as early as 10 Aug. (Eklund 1945); Enderby Land, 6 Oct. (Falla 1937); Bay of Whales, 6 Oct., 31 Oct. in two seasons (Siple & Lindsey 1937); C. Hallett, 31 Oct. (Maher 1962). Males usually arrive first and dig out sites, using bills and feet. Pre-laying exodus in second half of Nov.; 12 days for males, 18 days for females; also more complete for females; some males continue to visit and clear sites during period (Isenmann 1970). Females return a few hours before laying. At C. Hallett, first occupied nests, 9 Nov., but no eggs found (Maher 1962); at Enderby Land, nests occupied, 22 Oct. (Falla 1937). Laying dates from 25 Nov. (Clarke et al. 1913); most records in Dec. In Enderby Land, recently laid eggs, 3 Dec.; most nests had eggs, 9 Dec. (Falla 1937); in King Edward VII Land, eggs in early stages of incubation, Dec. 19 (Siple & Lindsey 1937). Chicks seen from 7 Jan.; S. Sandwich Is, eggs newly hatched and starting to hatch, 7 Jan. (Cowan 1983); Dronning Maud Land, one newly hatched chick, 10 Jan. (Lovenskiold 1960); Enderby Land, first chick found, a few days old, 11 Jan. (Falla 1937). Chicks almost ready to fly: Enderby Land, 13 Feb. (Falla 1937); C. Hallett, 6 Mar. (Maher 1962). Young flying at sea seen 19 Mar. (Bierman & Voous 1950). Departure dates from breeding grounds from early Feb. to mid-May: McMurdo Sound, 8 Feb. (Wilson 1907); Bay of Whales, 13 Mar. (Siple & Lindsey 1937); Palmer Pen., 15 May (Eklund 1945). Large number flying E to W in Enderby Land, 27 Apr. (Falla 1937).

On cliffs, steep slopes; in crevices, usually <1SITE

	AL		A
JFMA		MJJAS	O'N D

clefts; occasionally on open or partly open ledge or flat rock under overhang (Isenmann 1970; Cowan 1979). Usually face into prevailing wind at coastal colonies but not consistently so at Davis (Brown 1966); at mountain colonies may be protected from wind (Lovenskiold 1960; Loy 1962) or on cliffs facing north (Eklund 1945). Temperatures and windspeed greatly ameliorated in nests (Mougin 1968). Greatest density of nests over 65 m above general level of terrain where least liable to be snowed up.

NEST, MATERIALS Nil. Stones, sand, feathers, dead chicks, old eggs and excreta in scrapes probably adventitious; films or masses of vomit and excreta in grey hard layers may build up round scrape to 9 kg in weight (Lovenskiold 1960).

EGGS Ovoid to somewhat elongate; smooth, some pitted with irregular granular areas; mat; white. MEASUREMENTS:

Davis: 56 (51-59; 21) x 39 (37-42) (Brown 1966);

Dumont d'Urville: 59 (53-67; 40) x 42 (39-44) (Isenmann 1970);

C. Denison: 54.6 (52.6-60.4; 12) x 39.7 (38.3-41.5) (Falla 1937).

WEIGHTS:

Davis: 47 g (41-55; 21);

Dumont d'Urville: 57 g (45-73; 40).

CLUTCH-SIZE One. No replacement after loss. Doubtless single brooded.

LAYING Well synchronized, e.g. 27 Nov. to 13 Dec. generally. Egg laid between 20:00 and 24:00 (Prévost 1953) or during very early morning (Isenmann 1970).

INCUBATION By both parents in alternate shifts: first shift almost always by male, which takes longer shifts than female; shifts shorten towards hatching (Isenmann 1970). Non-incubating partner may visit and leave without relieving; sitting bird may leave before relief or leave promptly on relief; egg may survive a few hours of neglect; change-over usually at 'night' (Brown 1966). Average length of shifts: at Davis, 8.2 days (males), 6.2 days (females); at Dumont d'Urville 6 days (males), 5.5 days (females). Either parent may be sitting at hatching. Eggshell remains in nest. INCUBATION PERIOD. At Davis and Mawson: 43 days (41-44; 20); at Dumont d'Urville: 45 days (42-49; 31; two seasons combined).

YOUNG Semi-altricial, nidicolous. Hatched with lavender-grey down, eyes open, unable to stand. Pipping (at large end of shell) to emergence 2.4 days (Brown 1966). Rests for several days after hatching but can vomit at intruder by end of brooding stage. Brooded by both parents alternately for 2-10 days, usually 4-7. Some chicks, left alone within 1-2 days of hatching, may survive, shivering incessantly. After brooding stage, parents may stay at nest for 1-4 days (Mougin 1968, 1975). Fed by both parents by incomplete regurgitation, usually between 16:00 and 10:00 (Isenmann 1970); 6-7 feeds in first 10 days after hatching; length of feeding visits shorten during nestling period, down to a few minutes. NESTLING PERIOD: at Dumont d'Urville: 46.5 days (43-50; 30; for two seasons combined; Isenmann 1970); 48 days (41-53; 35; for two seasons combined; Mougin 1968). At Mawson 51 days (48-54; 7; Brown 1966).

Weight at hatching: Dumont d'Urville: GROWTH m from entrance; under boulders; in vertical or horizontal averages 40 and 42 g (34-58; 6+; Isenmann 1970; Mougin 1968). Rapid gain for first 24 days to *c*. 400 g, then slower to maximum (av. 500–550 g) at av. 36 days (26–39; 14; Prévost 1964), then decrease; weight at departure av. 365 g (Mougin 1968, 1975). Body, legs, bill grow rapidly for first half of period, then slowly and almost stop by departure; wings, tail accelerate growth till just before departure, continue slowly afterwards. At departure: measurements (av. local adults): wing 250 (295); tail 105 (115); tarsus 37.6 (37.8); culmen 21.4 (23.6) (Mougin 1975). Primaries appear at 10 days old, burst sheaths at 13 days. Fully fledged at 46 days, when young leave; departure during darkness, and then independent of parents.

SUCCESS Av. loss of eggs 44% (13–76); of chicks 18% (9–56); total loss 52% (23–77); varying with severity of weather (Brown 1966; Mougin 1975) and experience of parents; experienced birds twice as successful as inexperienced, 64 v. 31% (Mougin 1968, 1975; Guillotin & Jouventin 1980). Eggs lost by desertion, mainly early in incubation, by breaking, by snow. Chicks lost mainly in first 10 days, by starvation, freezing. Particularly heavy predation by skuas *Catharacta* reported at inland colonies but partly perhaps of dead chicks.

PLUMAGES

ADULT (1+) Definitive; basic. White. HEAD AND NECK. Small patch of *c*. 20 black bristles immediately in front of and above eye, similar to that of fulmar *Fulmarus glacialis* described by Zonfrillo (1982). UPPERPARTS. Feathers may have very pale-grey vermiculations shaped like growth bars; only visible on close inspection. TAIL. Rectrices may have very pale-grey vermiculations like those on upperparts. UP-PERWING. Coverts may have very pale-grey vermiculations like those on upperparts. Primaries have slight grey wash, and grey (84) tips of varying size sometimes present on p9 and p10. Bases of feather shafts cream (54) to ivory; most extensive on remiges.

DOWNY YOUNG (1) Mostly pre-pennaceous. Two forms known: (1) dorsal surface and crown covered by thick medium-grey (84) down; ventral surface, light grey (85) with pale grey (86) belly; (2) forehead grey-white; rest of dorsal down between light (85) and pale (86) grey; chin, flanks, upperparts and wings, pale grey (86); lower breast, belly and vent, white. Brown (1966) found both forms at Mawson and Casey, latter being rather uncommon. These descriptions based on skins and photographs of birds in protoptile; mesoptile appears similar although Watson (1975) considered it slightly paler. No information on mesoptile in common form.

JUVENILE (1) Juvenal. Similar to adult, but greyish barring on upperparts slightly more extensive and grey wash on primary tips may be more extensive (Watson 1975). These characters may be shared by some adults (Brown 1966; Watson 1975) so ageing can be doubtful. Bierman & Voous (1952) confident in identification of juveniles on this character, but found some 'intermediate' birds that they were unable to age.

BARE PARTS Two subspecies similar. Based on labels in MV and NMNZ, Mathews (1928), Falla (1937), Bierman & Voous (1950), Brown (1966) and photos in Lindsey (1986).

ADULT Bill, black (89) with bluish to white tinge on tomia near gape, often with violet-grey to flesh spot at base of latericorn. Some birds have lilac sulcus. Iris, blackish-brown. Legs vary from light bluish-grey to dark slate-grey, sometimes with brownish toe joints. Bird with pinkish drab tarsus also photographed (Lindsey 1986). Webs, light to pinkish grey; birds with dark grey tarsi often have dark grey webs. Outer edge of fourth toe is darkest part of foot. Claws, black.

DOWNY YOUNG Bare parts similar in both forms. Bill: maxilla black from tip to nostril, becoming gradually lighter towards gape. Nostril, slate-grey. Egg-tooth, white. Mandibular unguis, white; rest of lower mandible black, becoming gradually paler towards gape. Iris, milky blue. Legs, dark grey; webs, light pinkish grey; claws, black with white tips. Bill changes to adult colour in c. 10 days; adult iris colour attained in c. 50 days (Brown 1966).

JUVENILE As adult.

MOULTS No data to suggest *P.n. nivea* and *P.n. confusa* have different moult strategies.

POST-BREEDING Pre-basic. Breeding birds begin outwards primary moult about fledging period, late Feb. to early Mar. (Brown 1966; Beck 1969; this study in NMNZ). Inner primaries apparently replaced in rapid succession; skin of confusa from Balleny Is (NMNZ, collected 9 Mar. 1964) showed that inner four primaries had been dropped practically simultaneously. Body-moult begins during incubation, and continues during primary moult (Maher 1962; Beck 1969). Body-moult starts as early as Nov. in some, but not all. birds (Maher 1962; Brown 1966). Little data on secondary moult; on specimen mentioned above, outermost secondary on one wing was partly grown; all other secondaries old. Nonbreeders moult earlier; outwards primary moult begins in Jan. or possibly earlier (Brown 1966; Maher 1962), proceeds during non-breeding exodus, and complete, or almost so, in late Mar. to Apr. (Bierman & Voous 1952; Brown 1966; Beck 1969, 1970; this study). Body-moult also takes place during this period; two birds at Platcha in late Apr. 1961 had recently completed body-moult. Secondaries and coverts dropped by non-breeders found on 3 Jan. 1962 (Brown 1966). Rectrixmoult practically simultaneous (Bierman & Voous 1952; this study), beginning when primary moult complete or almost so.

POST-JUVENILE First pre-basic. Very little information. Juvenile (aged by Brown 1966) collected by Gould in 'the s. seas off Aust.', probably between 18 Aug. and 18 Sept. 1838 (Hindwood 1938) was completing primary moult [(Nx7) (4x1) (3x1) (2x1)] but showed little body-moult. No publications describe method for identifying 2-year-old birds on breeding grounds, which suggests that dorsal plumage of juvenile replaced in first year.

PRE-JUVENILE See Brown (1966) and Mougin (1975) for notes on plumage development.

MEASUREMENTS Measurements on live or recently dead specimens unless otherwise stated. (1) Balleny Is, recently dead, skins used for 8TH P (NMNZ). (2) Dumont d'Urville; WING from Jouventin & Viot (1985); other measurements from Prévost (1969). (3) Signy I., S. Orkney Is (Croxall 1982). (4) C. Hunter (Isenmann 1970). (5) C. Denison (Falla 1937). (6) C. Hallett, skins (Maher 1962). (7) Bluff I., skins used for TAIL and 8TH P (Brown 1966; TAIL and 8TH P from MV). (8) Anchorage I., as for Bluff I. (Brown 1966; TAIL and 8TH P from MV). (9) Svarthamaren, Queen Maude Land (Haftorn *et al.* 1988). (10) Casey (Cowan 1981). (11) S. Sandwich Is (Cowan 1983).

		MALES	FEMALES
WING	(1)	302.9 (4.79; 294-311; 18)	295.4 (5.24; 285-301; 8)
	(2)	296.6 (9.3; 268-315; 45)	284.1 (9.1; 263-295; 19)
	(3)	278 (6; 18)	270 (6; 21)
	(4)	276 (12; 5)	271 (12; 5)
	(5)	264.7 (6.45; 250-275; 15)	262.2 (3.87; 257-268; 5)
	(6)	267.2 (6.46; 249-280; 22)	256.5 (5.84; 257-277; 11)
	(7)	263.7 (2.49; 261-268; 6)	259.3 (6.37; 253-272; 6)
	(8)	268.8 (3.78; 261-269; 4)	255.8 (2.28; 252-258; 4)
OTTLE	(9)	258.3 (3.87; 253-264; 5)	253.3 (5.26: 245-258; 5)
8TH P	(1)	201.4 (5.79; 193-211; 16)	194.8 (3.80; 191-201; 6)
TAIL	(1)	135.2 (3.22; 130–142; 18)	133.6 (3.28; 130-140; 8)
	(5)	112.7 (4.64; 100-120; 15)	110.4 (3.88; 105-115; 5)
DULL	(6)	114.8 (3.79; 106-121; 22)	113.0 (3.70; 107-122; 11)
BILL	(1)	25.8 (1.02; 24.1-27.8; 19)	23.3 (0.72; 22.1-24.8; 8)
	(3)	22.3 (1.1; 18)	20.2 (1.1; 21)
	(4)	22.5 (1.8; 3)	21.4 (2.0; 5)
	(5)	20.7 (1.19; 18.5-21.5; 15)	20.7 (0.68; 20-21.5; 5)
	(6)	20.4 (0.78; 18.9–21.5; 22)	18.9 (1.02; 17.5-20.7; 11)
	(7)	20.9 (0.42; 20.5-21.8; 6)	19.8 (0.57; 18.8-20.5; 6)
	(8)	20.5 (0.57; 20-21.3; 4)	18.8 (0.50; 18–19.4; 4)
TIII	(9)	20.0 (0.37; 19.4-20.4; 5)	18.8 (0.38; 18.4–19.4; 5)
THL TARSUS	(9)	68.0 (1.15; 66.6-69.3; 5)	65.4 (0.92; 64.2-66.6; 5)
TARSUS	(1)	40.5 (1.30; 38.6-42.9; 19)	38.5 (1.50; 35.5-40.7; 8)
	(3)	38.2 (1.3; 18)	37.2 (1.2; 21)
	(4)	35.2 (2.7; 3)	34.1 (3.3; 5)
	(5)	32.4 (1.50; 30-36; 15)	32.2 (1.17; 31-34; 5)
	(6)	34.1 (1.13; 31.9-37.2; 22)	33.1 (1.36; 30.6-35.5; 11)
	(7) (8)	32.4 (0.73; 31–33; 6) 33.4 (1.49; 31.5–35; 4)	32.3 (0.69; 31-33; 6)
TOE	(1)	50.9 (1.08; 48.4-52.4; 19)	32.3 (0.83; 31-33; 4)
TOL	(5)	41.9 (1.53; 39-44; 15)	48.0 (2.15; 38.5-44; 5)
	(6)	41.7 (1.73; 37.9-44.2; 20)	42.5 (2.15; 38.5-44; 5) 41.4 (1.35; 38.5-42.8; 8)
	(7)	44.3 (1.04; 43.5-46; 6)	44.5 (1.00; 43.5-46; 6)
	(8)	45.1 (1.03; 44-46; 4)	44.0 (0.82; 43-45; 4)
Peorel P JDr. stary	RIGHI	UNSEXED	icker neck, on slimmer
WING	(10)	c. 276 (240-320; 178)	Micequel vertable 1:52
brownish	(11)	276 (265-285; 10)	
BILL	(2)	23.8 (19.0-27.8)	
	(10)	c. 22.1 (18-27; 178)	
	(11)	21 (18-23; 10)	
TARSUS	(2)	37.3 (30.0-42.5; 91)	
	(10)	36.3 (31-44; 178)	
	(11)	34.8 (33-37; 10)	

Great variation in size (see Geographical Variation).

WEIGHTS Measurements on live or recently dead specimens. (1) Balleny Is (NMNZ). (2) Dumont d'Urville (Jouventin & Viot 1985). (3) Signy I., S. Orkney Is (Croxall 1982). (4) C. Hunter (Isenmann 1969). (5) C. Denison (Falla 1937). (6) C. Hallett (Maher 1962). (7) Bluff I. (Brown 1966). (8) Anchorage I. (Brown 1966). (9) Svarthamaren, Queen Maude Land (Haftorn *et al.* 1988).

	MALES	FEMALES
(1)	367.2 (91.51; 345-490; 17)	341.0 (18.87; 317-370; 8)
(2)	439 (52.1; 320-550; 45)	358.2 (37.5; 263-295; 19)
(3)	341 (30; 20)	293 (25: 20)
(4)	317 (85; 3)	291 (48; 5)
(5)	332 (18; 7)	244 (17; 4)
(6)	276 (28.16; 226-312; 14)	263 (25.11; 229-302; 6)

(7)	268:5 (19.20; 248.3-295.5; 6)	246.2 (15.9; 230.1-274.9; 6)
(8)	292.7 (17.65; 266.8-306.3; 4)	246.2 (20.75; 219-262.7; 4)
(9)	258 (19.54; 237-278; 5)	229.8 (32.76; 200-283; 5)

Pagodroma nivea

409

No information on seasonal changes. Croxall (1982) suggests loss of weight during short incubation shifts unlikely to exceed *c*. 40 g.

STRUCTURE Wing, long and narrow, shaped as other fulmarine petrels. Eleven primaries; p11 minute, p10 longest. In *P.n. confusa*, p9 2–10 shorter, p8 9–27, p7 25–44, p6 44–63, p5 65–87, p4 91–111, p3 112–132, p2 140–156, p1 158–170. In nominate *nivea* p9 4–7 shorter, p8 15–22, p7 33–42, p6 53–60, p1 160–168. About 16 secondaries (A.N. Cowan). Twelve rectrices, t1 20–25 longer than t6. Bill short, laterally compressed; bill length about twice depth and three times width. Nostril tubes about one-third length of bill; oval nostrils face forwards and upwards. Tip of unguis touches line subtended by ventral base of maxillary unguis and ramicorn. Tibia and tibio-tarsal joint, feathered; tarsus, scutellate. Hind toe rather large.

GEOGRAPHICAL VARIATION Two subspecies recognized on basis of measurements: *nivea* and *confusa*. Falla (1937) suggested wing-length of 280 mm as arbitrary cut-off between the two. This widely accepted, because wing not as subject to sexual dimorphism as other measurements (Croxall 1982). On this basis, 'pure' colonies of subspecies *confusa* known from Balleny Is, and 'pure' colonies of nominate *nivea* from Davis, S. Georgia, C. Denison and Svathamaren (Falla 1937; Jouventin & Viot 1985; Haftorn *et al.* 1988). Most colonies mixed (e.g. Terre Adélie, C. Hallett, C. Hunter, Casey, S. Orkney Is, Proclamation Rock), with great variation in size within each colony and differing proportions of each subspecies between colonies (Jouventin & Viot 1985).

Starch-gel electrophoresis shows genetic variation to be high in Terre Adèlie. Jouventin & Viot (1985) suggest Snow Petrels forced from Antarctic continent in last glaciation, and differentiated in two refugia; *confusa* in higher latitudes (perhaps Balleny Is) and *nivea* in lower latitudes. Both have re-colonized Antarctica and there is now huge zone of hybridization.

Mathews (1928) noted that *confusa* had smaller eye-patch than *nivea*. This applies to large series of *confusa* from Balleny Is (NMNZ), in which eye-patch has only *c*. 10–15 bristles (see figure). However, Jouventin & Viot (1985) found no correlation between size of eye-patch and wing-length in Terre Adélie. DIR

REFERENCES

- Ainley, D.G., & R.J. Boekelheide. 1983. Studies avian Biol. 8: 2-23.
- Ainley, D.G., et al. 1978. Wilson Bull. 90: 492-510.
- Ainley, D.G., et al. 1984. AOU orn. Monogr. 32: 1-97.
- Ardley, R.A.B. 1936. Discovery Rep. 12: 349-76.
- Ardus, D.A. 1964. Br. Antarct. Surv. Bull. 3: 17-20.
- Armstrong, T., et al. 1973. Illustrated Glossary of Snow and Ice.
- Beck, J.R. 1969. Br. Antarct. Surv. Bull. 12: 33-44.
- Beck, J.R. 1970. Pp. 542-50. In: Holdgate 1970.
- Bennett, A.G. 1920. Hornero 2: 25-34.
- Bierman, W.H., & K.H. Voous. 1950. Ardea Spec. no.: 1-123.
- Bowra, G.T., et al. 1966. Br. Antarct. Surv. Bull. 9: 63-70.
- Brook, D., & J.R. Beck. 1972. Br. Antarct. Surv. Bull. 27: 131-7.
- Brown, D.A. 1966. ANARE Scient. Rep. Ser. B, (1) 89.
- Clarke, W.E. 1906. Ibis (8)6: 145-87.

Clarke, W.E., et al. 1913. Rep. Scient. Results Scot. natn. Antarct. Exped. 4: 199-306. Cline, D.R., et al. 1969. Auk 86: 701-16. Cowan, A.N. 1979. Aust. Bird Watcher 8: 69-90. Cowan, A.N. 1981. Notornis 28: 169-88. Cowan, A.N. 1983, Notornis 30: 250-2. Cox, J.B. 1976. S. Aust. Orn. 27: 26-82. Croxall, I.P. 1982, Notornis 29: 171-80. Croxall, I.P., et al. 1984. ICBP Tech. Publ. 2: 131-7. Derenne, P., et al. 1974. Com. natn. fr. Rech. Antarct. 33: 57-87. Dupond, C. 1946. Oiseaux 1-92. Eklund, C.R. 1945. Proc. Am. Phil. Soc. 89: 299-304. Enticott, J.W. 1986. S. Afr. J. Ant. Res. 16: 25-8. Falla, R.A. 1937. Rep. B.A.N.Z. Antarct. Res. Exped. Ser. B., II. Gain, L. 1914. Deux. Exped. Antarct. Fr. 1908-1910: 1-200. Gilchrist, A. 1952. Emu 52: 201-205. Griffiths, A.M. 1982. Cormorant 10: 9-13. Griffiths, A.M. 1983. Ardea 71: 145-50. Guillotin, M., & P. Jouventin. 1980. Gerfaut 70: 51-72. Haftorn, S., et al. 1988. Condor 90: 484-6. Hale, H.M. 1952. Rep. B.A.N.Z. Antarct. Res. Exped. Ser. B. 6: 21-36. Harper, P.C. 1987. Notornis 34: 169-92. Harper, P.C., et al. 1984, ICBP Tech. Publ. 2: 593-608. Harper, P.C., et al. BIOMASS Handbook 24: 1-22. Hindwood, K.A. 1938. Emu 38: 95-118. Holdgate, M.W. (Ed.). 1970. Antarctic Ecology. Hyett, J. 1974. Aust. Bird Watcher 5: 245. Isenmann, P. 1970. Oiseau Revue fr. Orn. 40 (Spec. no.): 99-134. Johnstone, G.W., et al. 1973. ANARE Scient. Rep. B, (1) 123. Jouventin, P. 1977. Condor 79: 498-9. Jouventin, P., & J.P. Robin. 1984. Emu 84: 46-8. Jouventin, P., & C.R. Viot. 1985. Ibis 127: 430-41. Jouventin, P., et al. 1984. ICBP Tech. Publ. 2: 609-25. Korotkevich, Y.S. 1959. Problems Arctic Antarct. 1: 95-108.

Lindsev, T.R. 1986. The Seabirds of Australia. Lovenskiold, H.L. 1960. Ibis 102: 132-4. Lowe, P.R., & N.B. Kinnear. 1930. Zoology 4: 102-93. Loy, W. 1962. Gerfaut 52: 626-40. Maher, W.I. 1962. Condor 64: 488-99. Mathews, G.M. 1928. Birds of Norfolk and Lord Howe Island and Australian South Polar Ouadrant, London, Montague, T.L. 1988. Hydrobiologia 165: 227-37. Mougin, J-L. 1968. Oiseau Revue fr. Orn. 38 (Spec. no): 1-52. Mougin, J-L. 1975. Com. natn. fr. Rech. Antarct. 36: 1-195. Nudelman, A.V. 1962. Soviet Antarctic Expeditions 1959-1961. Parmalee, D.F., et al. 1977. Antarct. J. US 12: 14-21. Perkins, J.E. 1945. Proc. Am. Phil. Soc. 89: 270-84. Prévost, J. 1953. Alauda 21: 205-22. Prévost, J. 1963. Terre et Vie 17: 35-49. Prévost, J. 1964. Oiseau Revue fr. Orn. 34 (Spec. no.): 91-112. Prévost, J. 1969. Oiseau Revue fr. Orn. 39 (Spec. no.): 33-49. Pryor, M.E. 1968. The Avifauna of Haswell Island, Antarctica. Ridoux, V., & C. Offredo. 1989. Polar Biol. 9: 137-45. Rootes, D.M. 1988. Br. Antarct. Surv. Bull. 80: 87-119. Routh, M. 1949. Ibis 91: 577-606. Ryan, P.G., & B.P. Watkins. 1988. Cormorant 126: 34-40. Rymill, J. 1938. Southern Lights, The Official Account of the British Graham Land Expedition 1934-1937. Siple, P.A., & A.A. Lindsey. 1937. Auk 54: 147-59. Sziji, L.J. 1967. Auk 84: 366-78. Van Autenboer, T. 1962. La Géographie 3: 93-108. van Franeker, J.A., & T. Montague. 1987. Corella 11: 37-43. Wace, R.H. 1921. Hornero 2: 194-204. Watson, G.E. 1975. Birds of the Antarctic and Sub-Antarctic. Watson, G.E., et al. 1971. Antarct. Map Folio Ser. 14. Wilson, E.A. 1907. Natn. Antarct. Exped. 1901-1904. Nat. Hist. II. Zoology, II, Aves: 1-121. Zink, R.M. 1981, Wilson Bull, 93: 1-20. Zonfrillo, B. 1982. Br. Birds 75: 225-7.





Volume 1 (Part A), Plate 27

Antarctic Petrel *Thalassoica antarctica* 1. Adult, ventral, fresh 2. Adult, dorsal, fresh 3. Adult, dorsal, worn

Snow Petrel *Pagodroma nivea* **4.** Adult, ventral

Southern Fulmar *Fulmarus glacialoides* 5. Adult, ventral 6. Adult, dorsal

Cape Petrel *Daption capense* 7. Adult, ventral 8. Adult, subspecies *capense*, dorsal 9. Adult, subspecies *australis*, dorsal

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