

Order SPHENISCIFORMES

Family SPHENISCIDAE penguins

Well-defined group of flightless, medium-sized to large seabirds of s. hemisphere, highly specialized for marine life. Closest affinities with procellariiforms. Divergence from common ancestor happened probably by late Eocene c. 45ma, when specialized anatomy was fully developed (Simpson 1975). Seventeen or nineteen species in six genera, depending on treatment; except for genus *Spheniscus* (four species), all breed in our region. Though popularly associated with s. polar region, most species breed on subantarctic and even cool temperate islands and the species of *Spheniscus* breed on the coasts of South America and South Africa, N to the equator, in the Galápagos.

Large head, short neck and elongate body. Tail, short and wedge-shaped, with 14–18 stiff rectrices, but quite long in *Pygoscelis*; often used as a prop when standing on land. Legs short and stout with webbed feet, vestigial hind toe and large claws; set so far back that when on land, birds stand vertically, walk with upright waddling gait, and often prefer to toboggan on belly. Tarsus mostly feathered; area of bare skin near feet tends to be larger in penguins of warmer regions. When swimming, head is hunched into shoulders and feet trail behind, tucked against tail to form good streamlining. Feet and tail used to change direction but propulsion in water by wings so highly modified that they are always called flippers; lack normal remiges; wing bones much flattened and broadened; joint of elbow and wrist almost fused, forming rather rigid, strong, flat and narrow flippers. When swimming under water, move flippers in plane at right angle to long axis of body. Bill, generally straight, rather stout and slightly shorter than head; extremely heavy in *Eudyptes*. Mouth heavily lined with keratinous, backwardly-directed spines. Distinctive bill-plates in all species, as in petrels.

Long bones not pneumatic and airsacs reduced; this, with their short feathers, makes penguins only slightly lighter than the water they displace, reducing the energy needed for diving; gastroliths may also act as ballast. Physiological specializations for diving include an ability to reduce blood flow to muscles while underwater. Capacity to carry oxygen seems no better than that of other diving birds; mechanisms preventing 'the bends' unknown. Often swim fast enough to breathe by 'porpoising'; speed of swimming poorly known, but perhaps in some species 6–12 kph (Kooyman 1975). Heat-exchange system in flippers and legs, a well-defined fat-layer and low surface area – volume ratio improve thermal insulation in cold waters but, even so, probably cannot keep body temperature stable at sea for long without being active (Kooyman 1975). On land over-heating can be a problem, especially in lower latitudes.

Feathers highly specialized; short, with broad flat rachis, and closely spaced barbs, especially near rachis and tips; considerably less water-repellent than those of other waterbirds but probably prevent much water penetration (Rijke 1970); small downy after-feather forms a second layer of insulation. Efficiency underwater unknown. Feathers are not arranged in pterylea; the only apteria is the 'crissum' between the legs, used as brood-patch. Plumage blue-black to grey-blue above, and white below. Face and crown are often distinctive with long yellow to orange plumes or other colours on face; patterns of head are the most important characters for field identification at sea. Juveniles similar to adults but usually duller. Sexes similar; males larger with heavier bills. All species have one rapid complete moult per cycle; feathers replaced more or less simultaneously. Feed intensely at sea just before moult, putting on weight. Greater part of moult on land during 2–6 weeks when birds cannot swim, having impaired insulation, and must fast. Moult generally follows breeding in adults; in some *Spheniscus* species, precedes breeding. In cool temperate, subantarctic and Antarctic species, non-breeders moult first, successful breeders last; failed breeders may begin soon after eggs or chicks lost.

Restricted to cool oceanic waters of s. hemisphere, where distribution correlated with Antarctic currents. In low latitudes tend to feed within continental shelf. Usually wide post-juvenile dispersal; movements of thousands of kilometres can occur. Feed on crustaceans, fish and squid. Hunting mostly visual, may be helped by echolocation; mostly by day in shallow surface dives but nearly all can dive deep and long enough to follow any vertical daytime migrations of prey. Emperor Penguin has been recorded diving to 267m, and staying submerged for 18 minutes.

Most species fast for long periods during courtship, incubation, brooding and nesting; extreme is for 110–115 days by male Emperor Penguin while nesting in Antarctic winter, losing up to 45% of initial weight.

Highly social at sea and on land; have complex courting and mate-recognition behaviour; most developed in highly gregarious species such as *Pygoscelis* and some *Eudyptes*, in which densely packed colonies may contain tens of thousands of birds. Elaborate visual and vocal displays used to maintain small nesting territories.

Comfort behaviour: use of shade, panting, spreading of flippers to prevent overheating, tucking in of flippers when cold, and shivering.

Most species breed once a year, in spring and summer; breeding synchronized; best in subantarctic and some

Antarctic species; least in more temperate species. One species breeds over winter, and breeding cycle of King Penguin lasts longer than a year.

Monogamous, pair-bonds long-lasting and even lifelong. Breeding pairs well spaced or virtually solitary to dense colonies of thousands. Nests range from substantial piles of pebbles, debris and assorted materials to nothing in the Emperor Penguin that incubates its egg on its feet. Colonies on all sorts of terrain, near shore or at high altitudes well back, even many kilometres, from the sea, on ice and also in burrows, crevices or caves according to the species. Clutch-size, 1-2 white eggs; three eggs occasionally seen in some species but not satisfactorily proved to have been laid by one female. In eudyptids, the first chick is always noticeably smaller than the second, and the chick from the first egg invariably fails to survive unless that from the second egg is lost at an early stage. Eggs laid at intervals of 2-4 days. Both sexes incubate, except in the Emperor, in which only males incubate. Change-overs take place daily in some species or at long intervals in others. Incubation period varies from about 35 to about 65 days. The young are covered in down and brooded and guarded by both parents for varying periods before forming crèches; both parents feed the chicks by incomplete regurgitation, recognizing and feeding only their own chick, even when it has joined a crèche. Fledgelings independent of parents when they go to sea at different ages from about 6 weeks to about 6 months. First breeding, not before 2 years old in any species and often much longer.

Species of Antarctic and subantarctic are most abundant; temperate and tropical species less numerous; some populations worryingly small (e.g. Yellow-eyed). Adult survival (70-90%) low compared to other seabirds and may be inversely related to breeding success. Breeding success high in most Antarctic species, except in Emperor where only 19% of fledgelings survive first year.

Much uncontrolled taking of adults and eggs for food and bait by whalers and sealers, from eighteenth to early twentieth centuries, reduced or destroyed some populations, especially of King Penguins, in subantarctic and Antarctica; marked increases of some species in past 30 years, attributed to greater availability of krill following reduction of Antarctic whales. Effects of drift-netting unknown. In lower latitudes, some populations have declined through overfishing in inshore waters, human interference, and damage to breeding habitat.

REFERENCES

Kooyman, G.L. 1975. Pp 115-37. In: Stonehouse. 1975.
Rijke, R.M. 1970. *J. Exp. Biol.* 52: 469-79.

Simpson, G.G. 1975. Pp 19-41. In: Stonehouse. 1975.
Stonehouse, B. (Ed.) 1975. *The Biology of Penguins.*

Pygoscelis adeliae Adelie Penguin

Catarrhactes adeliae Hombron and Jacquinot, 1841, *Annals Sci. Nat. Paris* (2) 16: 320 — Terre Adélie, c. long. 140°E.

Named in honour of Mme Adélie Dumont d'Urville, née Pepin, who married Admiral J.S.C. Dumont d'Urville in 1815 and died in 1842.

MONOTYPIC

FIELD IDENTIFICATION Length 70 cm; flipper 160–185 mm. Characteristic medium-sized penguin of Antarctica. Black above and white below, with black face and distinctive white eye-ring. Bill, black with dull orange base; appears short because covered with feathers for half length. At sea, look for short dark bill, dark face, lack of head markings, and long tail often held above water. Same size as Chinstrap Penguin *P. antarctica* but smaller than Gentoo Penguin *P. papua*. Sexes similar, but females smaller. No seasonal plumage changes, but dorsal plumage fades to brown before moult. Juveniles, separable.

DESCRIPTION **ADULT.** In fresh plumage, head, cheeks and dorsal plumage, including tail, bluish black. Distinctive ring of white feathers round eye. Flippers, blue-black dorsally with thin white trailing-edge. Black chin and throat separated from pure-white underparts by sharp V-shaped demarcation. Underflipper white with thin blackish leading-edge and small dark area at tip. Bill feathered for half length, mainly black, with orange to brick-red at base. Iris brown. Legs and feet dull white to pink, soles black. No seasonal changes but bluish cast disappears and dorsal feathers fade to brownish before moult (Feb.–Mar.). **FLEDGELING.** Similar to adult, except chin and throat white (sometimes greyish). Border between black and white areas of head starts at gape and passes below eye. Eyelids black, become white during first year. Throat becomes black after moult (Feb.) at one year old and then indistinguishable from adult.

SIMILAR SPECIES Dark face without crests or patches above eye, and absence of breast-bands separates adult Adelie Penguins from all other medium-sized penguins. No other similar-sized penguin has characteristic white eye-ring or partially feathered bill. Fledgelings similar to recently fledged Chinstrap Penguins but Adelie Penguins have no white above eye and no black under chin. Partly feathered bill also distinguishes young Adelie Penguins from recently fledged *Eudyptes* penguins, which usually have more grey on chin and throat.

Breed in large colonies, some exceeding half a million. Very gregarious, both on land and sea. When going to sea, large groups collect at water's edge; much jostling and inspection of water, birds on shore and in water exchange calls before one bird enters water. Birds in first few ranks closest to water immediately follow, but birds at back may not and once again congregate at water's edge. Cautious departure may be because predatory Leopard Seals *Hydrurga leptonyx* are common round colonies. When approaching rocks, shore-ice or icebergs, to land, birds raise heads above water c. 20 m offshore, dive beneath water and then jump out to height of 2 m (Sladen 1958). Often land on feet, gripping surface with very long toenails. Momentum sometimes forces birds to run forward until they can stop; or, landing on their feet, they fall

onto breast and toboggan. On sloping shores, they land on their breasts and walk clear of water. On beaches, surf in on waves and scramble forwards. Walk with flippers in various positions; in strong winds or low temperatures flippers kept close to body; over rough ice or rocks, when they may hop, flippers held away from body for balance. Tobogganning is common form of movement over snow; feet used for propulsion, tail held horizontally with flippers touching snow alternately. When escaping from threat, movement of feet and flippers rapid. In water, propulsion by flippers; quick, agile turns aided by feet and long tail; birds porpoise, swimming several metres below surface, leaping out for up to 30 cm and re-entering within about one metre. Can travel at speeds of 25 km/h (Sladen 1958), but 5–10 km/h more usual (Croxall 1985). On surface of sea, head and tail held up, body low in water. In flocks at sea, birds constantly give contact calls.

HABITAT Circumpolar in pack-ice of Antarctic Zone; distribution limited to S by continental shelf-ice, to N by limit of pack-ice. Important factors determining occurrence: location of breeding colonies; location of Antarctic slope front; occurrence of persistent pack-ice. Concentrations round breeding colonies out to about 140 km. During Oct., when colonies re-occupied, range contracts towards breeding sites; in Feb., at high densities in outer pack-ice; after breeding, disperse from coast into residual pack-ice. Highest densities over Antarctic slope front; in summer, absent from pack-ice seaward of slope (Ainley *et al.* 1984). Prefer pack-ice to open water; swim in leads and pools (Stonehouse 1963; Cline *et al.* 1969). In Ross Sea, Ainley *et al.* (1984) found no evidence that particular ice-concentration was favoured, but possibly prefer medium pack-ice (38–62% ice cover) (Zink 1981). In some areas, noted to prefer heavy pack-ice; 70–100% ice cover, Weddell Sea (Cline *et al.* 1969); 62–100% cover, Prydz Bay (Montague 1988). Prefer old ice, especially where surface uneven (Zink 1981). Seldom found in open water (Cline *et al.* 1969; Zink 1981; Ainley *et al.* 1984); but occasionally occur where waters very productive, particularly near colonies or pack-ice, or when travelling to feeding areas or on migration (Ainley *et al.* 1984). Localized occurrences within pack may be determined by biological activity in water-column below (Zink 1981; Ainley *et al.* 1984). In Prydz Bay, as in Ross Sea and elsewhere, birds feed at continental shelf break where submarine banks and counter-flowing ocean currents increase productivity by upwelling and mixing, and euphausiids abundant (Whitehead *et al.* in press). May also forage at confluence of ocean currents near Signy I. (Lishman 1985b). In Terre Adélie, continental shelf is eroded forming deep submarine valleys, and both shallow and deep-sea habitats found within foraging range (Ridoux & Offredo 1989). At King George I., feeding areas up to 40 km offshore; birds seldom feed in bays

round island, except near drifting ice-fields and associated concentrations of krill (Jablonski 1985). In Prydz Bay, no significant differences in abundance over range of sea surface-temperatures from -2°C to 3°C or wind speeds from 0 to 50 km/h (Montague 1988).

Breed on Antarctic continental coast and islands S of Antarctic Convergence. Colonies anywhere the land is ice-free and accessible from sea; on rocky islands, peninsulas, ridges, knolls, beaches, hillsides, scree slopes, valleys, moraines and gravel terraces (Falla 1937; Harrington 1960; Johnstone *et al.* 1973; Muller-Schwarze & Muller-Schwarze 1975).

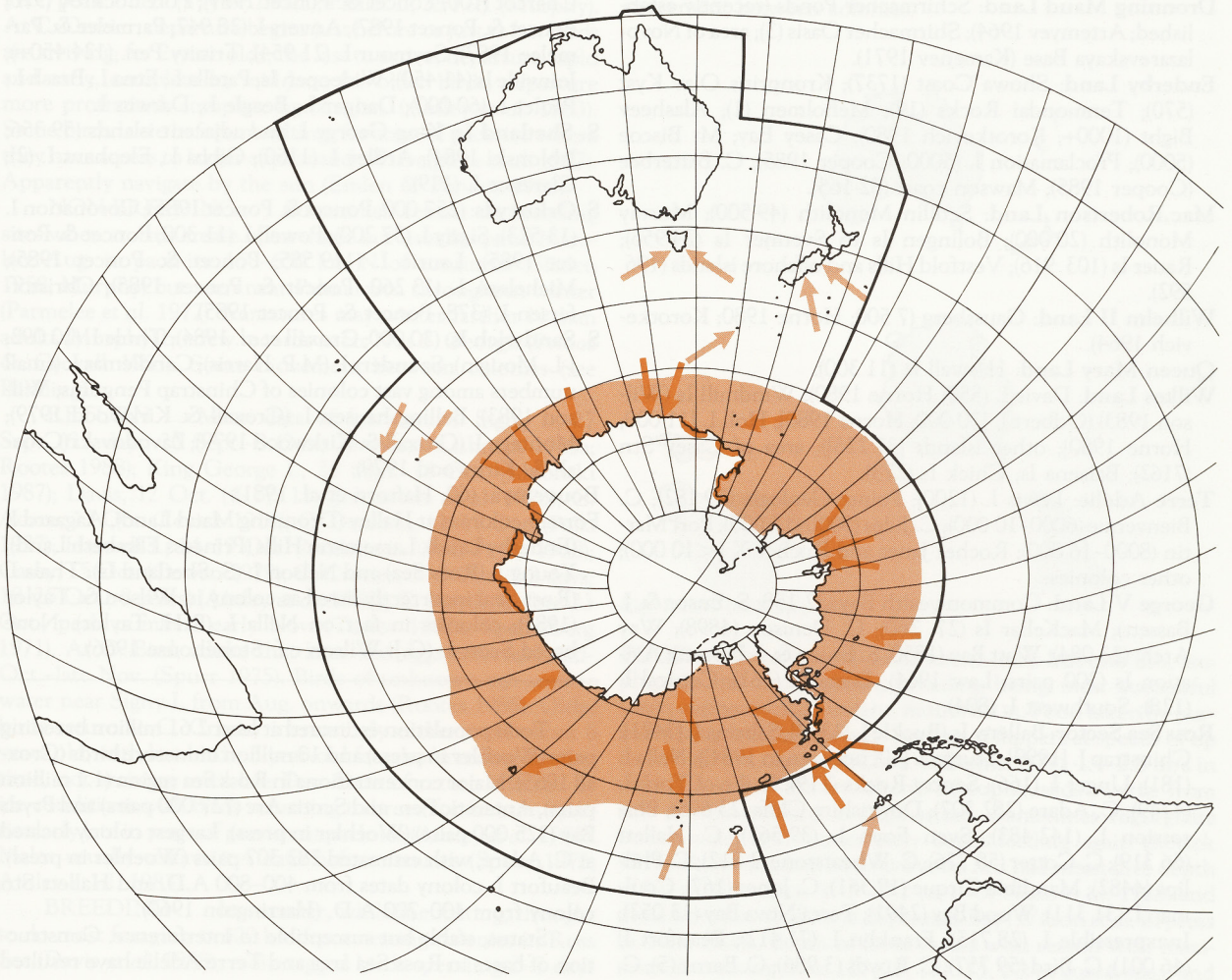
Landing sites for colonies on steep rocks, cliffs, or boulder or sand beaches (Falla 1937; Harrington 1960). Route to rookery often steep (Falla 1937) but free of high obstacles (Jablonski 1984). Moulting of some non-breeders takes place on rock or snow-slopes ashore, but most birds moult on floes and icebergs in pack ice (Falla 1937; Penney 1967), where concentrate on lee sides of hummocks and pressure ridges (Cline *et al.* 1969). Mean diving depth during early chick-rearing, 125 m (20; 79–175; 20); early crèche-stage, 118 m (29; 70–157; 11); late crèche stage, 84 m (19; 56–128; 20); prey may move upward as ice disperses late in breeding season (Whitehead 1989).

Disturbance or loss of habitat led to decline in numbers

at C. Hallett (Wilson *et al.* in press a), at C. Royds (Thomson 1977) and Terre Adélie (Jouventin *et al.* 1984) and proposed air-strip at Pointe Géologie will destroy breeding sites (Jouventin *et al.* 1984), but at some localities recovered by about 15 years after disturbance ended (Wilson *et al.* in press a; R.H. Taylor). Increase in numbers in outer Antarctic Pen. region in recent decades; reflects recovery from persecution or poorness of early estimates (D.G. Ainley), but also perhaps increased availability of krill as a result of whaling (Conroy 1975). Little expansion in continental colonies in S, where pack-ice restricted whaling (Conroy 1975). Development of fishing for krill is potential threat.

DISTRIBUTION AND POPULATION Circumpolar, rarely N of 60°S and generally found within limits of pack-ice; breeds on coasts and islands round Antarctica, and sparingly on n. islands such as S. Shetland, S. Orkney and S. Sandwich Is. Accidental to South America, Aust., NZ and subantarctic islands in Indian and sw. Pacific Oceans.

Pelagic range not well known. During breeding season populations concentrate near breeding colonies, in early summer ranging only about 140 km from them (Ainley *et al.* 1984) but probably range farther; at other times, rare beyond 60°S , the approximate outer limit of pack-ice; in Jan.-Feb., after breeding and during moult in Ross Sea, densities greatest



away from colonies in outer pack-ice (Ainley *et al.* 1984). Heard I. may be at fringe of normal pelagic range (Downes *et al.* 1959). Occasional records on subantarctic islands: Prince Edward Is, no records Iles Kerguelen; Heard I.; three, Sept. 1948; singles 25 Oct. 1949, 27 Oct. 1951, 21 Nov. 1953, 5 Jan. 1954 (Downes *et al.* 1959); Macquarie I.: 19 Nov. 1950 (Gwynn 1953) and Feb. 1964 (NZCL); S. Georgia, occasionally recorded: 11 Apr. 1977; 31 Oct–1 Nov. 1981 and two earlier records (Matthews 1929; Prince & Croxall 1983); Falkland Is, single Dec. 1961 (Woods 1975).

AUST. Accidental; two early doubtful records, both unacceptable: Cottesloe Beach, near Fremantle, WA, Apr. 1937, probably ship-assisted (Whittell 1937); Portland, Vic., July 1933 (Learmonth 1955). Valid records: Port Davey, Tas., 11 Jan. 1980 (Aust. RAC Record 16); Fortescue Bay, Tas., 25–31 Dec. 1983 (Tuffy & Fazackerley 1984).

NZ One beachcast, e. coast of Marlborough, SI, 22 Dec. 1962 (Kennington 1963).

BREEDING Round coasts of Antarctic continent and subantarctic islands; >60°S except Bouvetøya (most n. colony) and S. Sandwich Is. Most s. colony at C. Royds, Ross I. Summary of known breeding localities and population estimates from Woehler (in press) unless indicated (numbers are pairs unless indicated).

Dronning Maud Land: Schirmacher Ponds (recently established; Artemyev 1964); Shirmacher Oasis (3); area of Novolazarevskaya Base (Kamenev 1971).

Enderby Land: Showa Coast (1737); Kronprins Olav Kyst (570); Tenmondai Rocks (19); Meholmen (1); Alasheev Bight (1000+; Korotkevich 1980); Casey Bay; Mt Biscoe (5000); Proclamation I. (5000; Cooper 1985); C. Batterbee (Cooper 1985); Mawson coast (82 165).

Mac.Robertson Land: Scullin Monolith (49 500); Murray Monolith (20 000); Bolingen Is to Svenner Is (24 956); Rauer Is (103 916); Vestfold Hills and offshore islands (196 592).

Wilhelm II Land: Gaussberg (7 500; Horne 1980; Korotkevich 1964).

Queen Mary Land: Haswell Is (11 300).

Wilkes Land: Davis I. (550; Horne 1980); Windmill Is (Wilson 1983) (Odbert I. [20 000; Horne 1980]; Holl I. [11 000; Horne 1980]; other islands [37 225]); area of Casey Stn (7162); Balaena Is; Chick Is (273).

Terre Adélie: Lewis I. (1200); Pointe Géologie (29 182); C. Bienvenue (6000–10 000); C. Jules (5000–15 000); Port Martin (8000–16 000); Rocher Janet and Rocher X (<10 000); other colonies.

George V Land: Commonwealth Bay (32 158; S. Ensor & J. Bassett); MacKellar Is (27 260); C. Denison (4898); Way Arch. (23 084); Watt Bay (1850; S. Ensor & J. Bassett); Aviation Is (300 pairs; Law 1964); Dome I. (161); Conical I. (128); Southwest I. (804).

Ross Sea Sector: Balleny Is (Buckle I. [1360]; Sabrina I. [3471]; Chinstrap I. [1999]; Sturge I. [10, not seen in 1984]; Nella I. (181); Unger I. (166); Sentry Rocks (119); Duke of York I. (4749); C. Adare (282 307); Downshire Cliffs (23 695); Possession I. (142 483); Sven Foyne I. (39 567); C. Hallett (66 319); C. Cotter (58 776); C. Wheatstone (2 812); C. Phillips (4482); Mandible Cirque (19 361); C. Jones (167); Coulman I. (31 311); Wood Bay (2491); Terra Nova Bay (13 052); Inexpressible I. (28 715); Franklin I. (71 412); Beaufort I. (46 001); C. Bird (59 757); C. Royds (3 986); C. Barne (5); C.

Crozier (177 083).

Marie Byrd Land: Cruzen I. (100; Strandtmann 1978); Shepard I. (40 000; Strandtmann 1978); Siple I. (50 000); Maher I. (1100); Lauf I. (500).

Peter I Øy: (20; Holgersen 1951).

Antarctic Pen.: Charcot I. (50; Croxall & Kirkwood 1979); Marguerite Bay (1807+; Poncet & Poncet 1987); Cone I. (3000; Poncet & Poncet 1987); Chatos I. (100; Poncet & Poncet 1987); Adelaide I. and adjacent islands (45 850; Poncet & Poncet 1987); Ginger I. (3000; Poncet & Poncet 1987); Emperor I. (700; Poncet & Poncet 1987); Pourquoi Pas I. (700; Poncet & Poncet 1987); Lagotellerie I. (1700; Poncet & Poncet 1987); Red Rock Ridge (1200; Poncet & Poncet 1987); Barcroft (1600; Poncet & Poncet 1987); Lavoisier (150; Poncet & Poncet 1987); Andressen I. (2200; Poncet & Poncet 1987); Detaille I. (900; Poncet & Poncet 1987); Holdfast Pt (625; Poncet & Poncet 1987); Armstrong Reef (12 800; Poncet & Poncet 1987); Darbel I. (650; Poncet & Poncet 1987); C. Evensen (1200; Poncet & Poncet 1987); Pitt I. (4400; Poncet & Poncet 1987); Fizkin I. (250; Poncet & Poncet 1987); Fish Is (4000; Poncet & Poncet 1987); Kim Is (1300; Poncet & Poncet 1987); Vieugué I. (1000; Poncet & Poncet 1987); Gerbache I. (250; Poncet & Poncet 1987); Yalour I. (8000; Poncet & Poncet 1987); Petermann I. (400; Poncet & Poncet 1987); Berthelot I. (1300; Poncet & Poncet 1987); Booth Is (1208+; Croxall & Kirkwood 1979); Port Charcot (100; Poncet & Poncet 1987); Port Lockroy (970; Poncet & Poncet 1987); Anvers I. (28 947; Parmelee & Parmelee 1987); Seymour I. (21 954); Trinity Pen. (124 450+); Joinville Is (41 450); Wideopen Is; Patella I.; Etna I.; Brash I.; Paulet I. (60 000); Danger I.; Beagle I.; Darwin I.

S. Shetland Is: King George I. and adjacent islands (59 356; Jablonski 1984); Ardley I. (1160); Gibbs I., Elephant I. (2); Clarence I. (119).

S. Orkney Is: (257 000; Poncet & Poncet 1985); Coronation I. (13 523); Signy I. (37 200); Powell I. (11 300; Poncet & Poncet 1985); Laurie I. (119 585; Poncet & Poncet 1985); Michelsen I. (13 260; Poncet & Poncet 1985); Christoffersen I. (378; Poncet & Poncet 1985).

S. Sandwich Is: (30 000; Croxall *et al.* 1984); Thule I. (10 092; J-L. Mougín); Saunders I. (M.P. Harris); Candlemas I. (small numbers among vast colonies of Chinstrap Penguins; Wilson 1983); Bellingshausen I. (Croxall & Kirkwood 1979); Montagu I. (Croxall & Kirkwood 1979); Zavodovski (Croxall & Kirkwood 1979).

Bouvetøya: (60; Haftorn *et al.* 1981).

Former colonies at Halley (Dronning Maud Land), Aagaard I. (Enderby Land), Larsemann Hills (Princess Elizabeth Land), Young I. (Ross Sea) and Nelson I. (S. Shetland Is). Thala I. (Ross Sea) incorrectly listed as colony in Wilson & Taylor (1984); colonies in fact on Nella I. (R.H. Taylor). None breed Scott I. (G.J. Wilson c.f. Stonehouse 1966).

Total population estimated at least 2.61 million breeding pairs (Woehler in press) and 10 million immature birds (Croxall 1985). Major concentrations in Ross Sea region (1.1 million pairs), Antarctic Pen. and Scotia Arc (727 000 pairs) and Prydz Bay (325 000 pairs) (Woehler in press). Largest colony located at C. Adare, with estimated 282 307 pairs (Woehler in press). Beaufort I. colony dates from 400–800 A.D. and Hallett Stn colony from 400–700 A.D. (Harrington 1960).

Status, stable but susceptible to interference. Construction of bases in Ross Sea area and Terre Adélie have resulted

in decline in numbers at nearby colonies. At C. Royds numbers decreased from 1600 to 1000 pairs in 4 years after construction of McMurdo Stn and Scott Base. Prohibition of flights by helicopters and of people walking through colony resulted in return to former numbers (Harper *et al.* 1984). Construction of base at Ile de Petrels, Terre Adélie, caused decline in local population (Jouventin *et al.* 1984). Numbers also declined in S. Orkney Is and other areas of Antarctic Pen. because birds were disturbed, harvested for pet-food and other factors; but remained stable where no human interference (Croxall *et al.* 1984; Jouventin *et al.* 1984). Recent increases at some sites, many where birds formerly persecuted; perhaps resulting from increase in krill as whale numbers have decreased (Volkman & Trivelpiece 1980). Ross Sea colonies may have increased in past 10–20 years but C. Royds the only colony surveyed consistently, and other trends probably spurious (D.G. Ainley).

MOVEMENTS Disperse N of pack-ice in winter with at least some dispersal round Antarctica.

DEPARTURE Adults left Signy I., Feb. (Rootes 1988); King George I., late Feb. (Jablonski 1987); C. Adare after moulting, 14 Mar. (Levick 1914); Paulet I., a few days after 15 Mar. (Murphy); Davis, 10–31 Mar. (Johnstone *et al.* 1973); Haswell I., late Mar. (Pryor 1968) to first 10 days. Apr. (Nudelman 1962). Juveniles leave earlier: C. Royds, 31 Jan.–25 Feb., peak 9 Feb. (Taylor 1962a); Paulet I., 28 Feb. (Murphy). At C. Crozier, departure begins just before or just as last birds are arriving; for 2-year-olds, the last to arrive, departure rapid and early, complete by mid-Jan.; for older birds, departure more protracted, complete by late Jan. (Ainley *et al.* 1983). Some birds leave before moulting, for zone of pack-ice where they have access to larger euphausiids (Trivelpiece *et al.* 1987). Apparently navigate by the sun (Emlen & Penney 1966).

NON-BREEDING Sometimes return to breeding sites when storms create open water but usually spend Mar.–late Aug. in pack-ice 150–650 km N of continent (Sladen 1958; Murphy) but seen near Palmer Stn throughout winter (Parmelee *et al.* 1977). Immatures may winter farther N than adults (Murphy) but few records as far N as S. Georgia (Prince & Croxall 1983). Some movement between colonies (see Banding).

RETURN Mean date of first return: Signy I., 27 Sept. (6.3 days; 20 Sept.–8 Oct.; 25 years) (Lishman 1985a; Rootes 1988); King George I., 28 Sept.–18 Oct. (Jablonski 1987); Davis, 12 Oct. (4–17; 11) (Johnstone *et al.* 1973); C. Adare, 13 Oct. (Levick 1914); C. Denison, 12–17 Oct. (Falla 1937); Haswell I., 14–19 Oct. (Nudelman 1962; Pryor 1968); Casey, 15 Oct. (Cowan 1979); C. Crozier, 20.9 Oct. (2.2 days; 18–25 Oct.; 8 years) (Ainley *et al.* 1983); C. Royds, before 23 Oct., peak numbers early Nov. (Taylor 1962a; Spellerberg 1971). At C. Bird, adults that later laid eggs returned mid-Oct.–late Nov. (Spurr 1975). Birds of unknown age seen in water near Signy I. from Aug. onwards (Rootes 1988). Older birds return to C. Crozier increasingly earlier until about 8 years old, with last birds, 2-year-old females breeding for first time, not arriving until late Dec. Date of return affected by ice-conditions with birds returning to breed for first time particularly late in years of persistent pack-ice (Ainley *et al.* 1983). Males usually return ≥ 4 days before females (Spurr 1975; Ainley *et al.* 1983).

BREEDING In summer, while incubating, thought to do most foraging > 100 km from nesting colonies in Ross Sea (Davis *et al.* 1988), radio-tagged birds spending 2–7 days

30–40 km from colony before heading rapidly N for > 150 km, returning 10–15 days later (Sadlier & Lay 1988). When feeding young, appear to stay closer to colony, radio-tagged birds being located repeatedly 15 (Sadlier & Lay 1988) to 50 km (Ward *et al.* 1986) from breeding colony at C. Bird, Ross Sea, but can travel up to 140 km (Ainley *et al.* 1984). Estimated to travel up to 120 km from Signy I. (Lishman 1985b), 165 km from King George I. (Jablonski 1985), though mostly < 50 km (Jablonski 1985; Trivelpiece *et al.* 1987), and 65.3 km from Palmer Stn, swimming at 11.2 km/h for 11.7 h (Obst 1985). When first returning to land may travel 100 km or more across ice with normal travelling speed on land 2.6–3.9 km/h (Taylor 1962b). On ice, travel at 0.9–3.9 km/h (Fedak *et al.* 1974) by either walking or tobogganning, the latter being energetically cheaper (Croxall 1985). Records of adults outside usual range usually spring and summer: Heard I., Sept.–Jan. (Downes *et al.* 1959); Tas., Dec.–Jan. (Tuffy & Fazackerly 1984; Aust. RAC Record 16). Pre-moult departure, late Jan.–early Feb. at C. Crozier (Ainley *et al.* 1978) with moult migration to zone of pack-ice (Trivelpiece *et al.* 1987). Yearlings often moult on land away from colonies in traditional sites that have protection from wind (Ainley *et al.* 1983).

BANDING All long distance recoveries BBL. Most distant recoveries from Ross Ice Shelf (at least six birds) summarized Fig. 1. Other recoveries from six different sites round Antarctica, all within 150 km of banding site, which shows movement between colonies.



Fig. 1. 80S 180E 1X1 BBL

FOOD Mostly euphausiid crustaceans but also fish, amphipods and cephalopods, breeding being most successful when euphausiids abundant. **BEHAVIOUR.** Food taken by pursuit-diving with synchronic beating of flippers at speeds of up to 1.98 m/s in captivity (Clark & Bemis 1979), 1.4–2.8 m/s in wild (Croxall 1985). In schools of euphausiids swerve from side to side pecking at high speed. Sometimes regurgitate under water and immediately begin feeding again (Levick 1914). Radio-tracked birds at Syowa Stn had mean dive depth of 8.0–10.0 m (max. 17.3–27.2 m; $n=3$; Naito *et al.* 1988) and dives were also shallow at Esperanza Bay (Wilson *et al.* in press b). Near Davis, depth of dives varied with season with maximum decreasing from 125 (20; 79–175; 27) in guard-stage and

118 (29; 70–157; 11) in early crèche-stage to 84 (19; 56–128; 20) in late crèche-stage (Whitehead 1989). Radio-tracked birds dived for 114.9 s (29.7; 72) while feeding, pausing for 44.6 s (35.2) between dives (assuming that dives <60 s were not feeding dives) and spent 42% of their time diving or feeding (Davis *et al.* 1988). Three other radio-tracked birds had mean diving times of 84–108 s (max. 222–336; Naito *et al.* 1988). Lishman (1985b) thought most foraging occurred at night and three radio-tracked birds dived most frequently between 16:00 and 20:00 (Naito *et al.* 1988). Mean feeding time per foraging trip 3.3 h (Trivelpiece *et al.* 1987). Eat snow while nesting, presumably for water, and will carry snow to partner on nest (Levick 1915).

NON-BREEDING No information.

BREEDING Diet while incubating summarized Table 1; while feeding chicks Tables 2, 3. At Davis (water-offloaded samples, 123 before hatching, 451 post-hatching; Puddicombe & Johnstone 1988) euphausiids *Euphausia superba* 66% freq. all samples, 1.33 cm carapace length (0.28; 0.62–1.90; 262), *E. crystallorophias* 76, 0.93 (0.12; 0.52–1.38; 343), mysidaceans <0.1% wt. all samples, 0.7% freq., amphipods 82.2% freq. (*Hyperia macrocephala* 40.8, *Hyperoche* 0.2, *Themisto gaudichaudii* 4.2, *Cylopus magellanicus* 38.9, *Eusirus perdentatus* 6.3, *E. sp. nov.* 23.2, *Paramoera walkeri* 1.9, *Cheirimedon fougnieri* 22.5, *Orchomene rossi* 32.9, *Uristes murrayi* 4.4, *Waldeckia obesa* 4.2, *Epimeriella macronyx* 9.2, *E. walkeri* 0.2), isopods <0.1% wt., 0.3% freq. (Valvifera), prawns <0.1, 0.2; fish 73.3% freq. (Myctophidae 0.2, *Pagothenia borchgrevinkii* 2.4, *Pagothenia cf. hansonii* 1.2, *P. sp.* 16.2, *Pleuragramma antarcticum* 36.2, unident. Nototheniidae 0.9, *Gymnodraco acuticeps* 0.9, *Chionodraco* 11.5, *Pagetopsis macropterus* 1.4, unident. Channichthyidae 4.2); pteropods <0.1% wt., 5.2% freq., other gastropods <0.1, 0.5, cephalopods <0.1, 0.9, polychaetes <0.1, 0.7 (*Tomopteris*), coelenterates <0.1, 0.2, holothurians <0.1, 0.2. At Davis in later years (62 samples; Green & Johnstone 1988) amphipods 69.8% freq. (max. 650 individuals) pre-hatching period, euphausiids 33.8 (*E. superba* 45.0% no. euphausiids, 10% freq., *E. crystallorophias* 55.0, 14), unident. crustaceans 15, fish 18, cephalopods 5. After hatching (70 samples) euphausiids 100% freq., *E. superba* 71.7% no. euphausiids, 97% freq., 3.93 cm (585), *E. crystallorophias* 28.3, 86, 2.80 cm (341), amphipods 23; fish 83 incl. *Pleuragramma antarcticum* 13.9 cm (1.7; 17), *Pagothenia*; cephalopods 9. In years when *E. crystallorophias* and fish are taken by birds feeding chicks, most feeding apparently inshore and breeding success higher than when they have to travel offshore to take *E. superba*. At King George I. (48 stomachs, 26 males, 22 females; Volkman *et al.* 1980) euphausiids 100% freq., 4.06 cm (SE 0.01; 1.0–5.7), amphipods <0.2, 1.98 cm (1.0–5.4), highly digested fish 13. Of the amphipods (n=80) were *Hyperia macrocephala* 4% no., *Themisto gaudichaudii* 78, *Cylopus lucasii* 1, *Eusirus* 13, *Eurymera monticulosa* 1, *Cheirimedon femoratus* 1, *Cyphocariscus richardi* 1, *Hippomedon kergueleni* 1 (Jazdzewski 1981). Other records from same site (219 312 g sample; Jablonski 1985) incl. mixture of euphausiids *E. superba* 79–100% wt. euphausiids, 3.3–5.7 cm (1608), *E. crystallorophias* 0–21, 2.1–3.6 cm (1221), length of euphausiids varying with site of capture. At Signy I. (28 stomachs; Lishman 1985b) *E. superba* 3.3 cm (n=2849); amphipods *Themisto gaudichaudii*, unident. Hyperiidae, *Cylopus batesi/lucasii*. Re-analysis into pre-hatch samples (15) and post-hatch (13; Croxall & Lishman 1987) summarized Tables 1, 2, 3. Earlier collections Signy I. (10; White & Conroy 1975) also almost entirely *E. superba* 3.67 cm (0.26; 3.2–4.1; 65) with

Table 1. Diet of Adelie Penguin while incubating

| Percentages | weight | | number 3 | frequency | |
|----------------------------|--------|------|-------------|-----------|-------|
| | 1 | 2 | | 1 | 2 |
| CRUSTACEANS | 96.4 | 95.6 | 98.6 | 100.0 | |
| Euphausiids | 54.6 | 17.3 | 98.3 | 99.4 | 34 |
| <i>E. superba</i> | 5.8 | 5.7 | 98.3 | 99.4 | 14 10 |
| <i>E. crystallorophias</i> | 48.8 | 6.8 | | | 46 14 |
| Amphipods | 41.8 | 63.9 | 0.3 | 0.6 | 94 68 |
| FISH | 3.5 | 4.0 | 1.4 | <0.1 | 20 18 |
| CEPHALOPODS | <0.1 | 0.4 | | | 5 |

(1) Davis (Puddicombe & Johnstone 1988). (2) Davis (Green & Johnstone 1988). (3) Signy I. (Lishman 1985b; Croxall & Lishman 1987).

Table 2. Diet of Adelie Penguin while feeding chicks (% weight [1–7], % volume [8]).

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|----------------------------|------|------|------|------|----|-----|------|------|
| CRUSTACEANS | 67.6 | 90.9 | 99.9 | 99.6 | 79 | 100 | 87.6 | 56.0 |
| Euphausiids | 66.5 | 90.7 | 99.6 | 99.2 | 79 | 100 | 72.7 | 46.0 |
| <i>E. superba</i> | 24.6 | 73.9 | | 99.2 | 41 | 100 | | |
| <i>E. crystallorophias</i> | 41.9 | 31.8 | | | 38 | | | 46.0 |
| Amphipods | 1.1 | 0.2 | 0.3 | 0.4 | <1 | | 3.9 | |
| FISH | 32.4 | 9.1 | 0.1 | 0.4 | 18 | | 7.0 | 44.0 |
| CEPHALOPODS | <0.1 | <0.1 | | | 3 | | | |

(1–7) % weight: (1) Davis (Puddicombe & Johnstone 1988). (2) Davis (Green & Johnstone 1988). (3) King George I. (Volkman *et al.* 1980). (4) Signy I. (Lishman 1985b). (5) Terre Adélie (Offredo *et al.* 1985; Ridoux & Offredo 1989). (6) Ardley I. (Valencia *et al.* 1988). (7) King George I. (Jablonski 1985).

(8) % volume: C. Bird (Paulian 1975).

Table 3. Diet of Adelie Penguin while feeding chicks (% number)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|----------------------------|------|------|------|----|------|----|------|------|
| CRUSTACEANS | 99.9 | 99.9 | 90.1 | 99 | 99.1 | 73 | 98.3 | 78.0 |
| Euphausiids | 99.7 | 99.5 | 89.0 | 99 | 99.1 | 72 | 97.3 | |
| <i>E. superba</i> | 98.1 | 99.5 | | 19 | <0.1 | 72 | 97.3 | |
| <i>E. crystallorophias</i> | 1.6 | | | 80 | 99.1 | | | 75.0 |
| Amphipods | 0.2 | 0.5 | 1.1 | <1 | 0.9 | 1 | 0.9 | |
| FISH | 0.1 | 0.1 | 9.4 | 1 | <0.1 | 27 | 1.7 | 22.0 |
| CEPHALOPODS | | | <0.1 | | | | | |

(1) King George I. (Volkman *et al.* 1980). (2) Signy I. (Lishman 1985b). (3) C. Crozier (Emison 1968). (4) Terre Adélie (Offredo *et al.* 1985; Ridoux & Offredo 1989). (5) C. Bird (van Heezik 1988). (6) C. Hallett (Croxall & Lishman 1987; F.C. Kinsky; P. Ensor). (7) C. Hallett (Croxall & Lishman 1987; L. Logan). (8) C. Bird (Paulian 1975).

a few amphipods as were those by Sladen (1958). At C. Crozier, Ross Sea (207 stomach-pumped samples, 230 100 food items; Emison 1968) euphausiids 100% freq. *Euphausia crystallorophias* 100, *E. superba* 30; fish 94.9 (<0.75 cm, 98.5% no.; 0.75–2.00 cm, 1.5%), amphipods 100; also hydrozoa and 2 cephalopods *Nototodarus sloani*. Fish were *Pleuragramma antarcticum* 8.4% no., *Chaenodraco wilsoni* and *C. hamatus* 1.0; amphipods (n=3492) *Hyperia macrocephala* 0.1% no., 70% freq., *H. macronyx* <0.1, 35, *Hyperiella dilitata* <0.1, 46,

Hyperoche medusarum <0.1, 5, *Eusirus microps* 0.1, 38, *E. perdentatus* <0.1, 16, *Paramoera walkeri* <0.1, -, *Cheirimon fougneri* <0.1, 3, *Ochomene rossi* 0.1, 92, *O. spp* 0.1, 70, *Orchomenella pinguides* <0.1, -, *O. plebs* 0.6, 89, *Uristes murrayi* <0.1, 14, *U. spp* <0.1, -, *Cyphocaris richardi* <0.1, 13, *Epimeriella macronyx* <0.1, 35. Males took larger euphausiids (0.9–2.9 cm) and fish (eye-lens diam. 0.08 cm) than females (euphausiids 1.0–2.7 cm, fish lens 0.06 cm; Ainley & Emison 1972). At **Terre Adélie** (105 adults; Offredo *et al.* 1985; Ridoux & Offredo 1989) crustaceans amphipods incl. *Hyperidea* 28% freq. (*Hyperia macrocephala*, *Hyperiella macronyx*, *Hyperoche*, *Themisto gaudichaudii*, *Cylopus*), Gammaridea (*Eusirus perdentatus*, *E. tridentatus*, *Orchomene*, *Uristes gigas*, *Waldeckia obesa*, *Epimeriella macronyx*), isopods, euphausiids *Euphausia superba* 81% freq., 4.3 cm (2.2–5.8), *E. crystallorophias* 94, 2.6 cm (1.0–3.4); fish *Trematomus newnesi*; cephalopods 18.1% freq. *Psychroteuthis glacialis*, wt. 13.9 g, max. 25 g; fish and *E. superba* taken mostly Jan.–early Feb. *E. crystallorophias* predominated late Feb.–early Mar. At **C. Bird**, Ross I. (16; van Heezik 1988) *Euphausia superba* 18.8% freq.; *E. crystallorophias* 87.5% freq., 2.1–2.9 cm, 276–41 938 individuals/bird; amphipods sp. 1: 0.2% no., 56.2% freq.; sp. 2: 0.7, 43.8; decapods <0.1, 6.3; fish <0.1, 6.3, all probably taken shortly before birds reached land. At **Ardley I.** (36; Valencia *et al.* 1988) *E. superba* 3.47–4.50 cm (1202 per stomach). At **C. Hallett** (76 samples, guard-stage; Croxall & Lishman 1987; Puddicombe & Johnstone 1988; F.C. Kinsky; P. Ensor) euphausiids *E. superba* large 77% freq., small 23, other crustaceans 3, fish 9; fish increasing in importance late in season. At **same site** (73 samples, crèche-stage; Croxall & Lishman 1987; L. Logan) euphausiids also *E. superba* 100% freq., other crustaceans incl. amphipods 62, fish 48. At **C. Bird** (15 chicks; Paulian 1975) euphausiids *E. crystallorophias* 2.90 cm (393).

Other records; near Casey Stn (27; Cowan 1983), euphausiids *Euphausia superba* 25.9, *E. crystallorophias* 44% freq., *E. sp.* 14.8, unident. euphausiids 11.1, amphipods *Hyperoche* 3.7, *Paramoera walkeri* 3.7, *Orchomene* 3.7; fish 11.1; in Ross Sea during summer (Ainley *et al.* 1984): continental slope (n=2) crustaceans 97.7% wt.: euphausiids *Euphausia superba* 99.0% no., 100% freq., 4.0 cm (0.3; 60), *E. crystallorophias* 0.3, 1.0, amphipods *Orchomene* 0.4, 100, unident. 0.1, 100 crustaceans; fish *Pleuragramma antarcticum* 2.3, 0.1, 100; continental shelf (n=3) crustaceans 99.9 euphausiids *E. crystallorophias* 99.6, 100, 2.0 (0.4; 48), amphipods *Orchomene* 0.2, 100; unident. crustaceans 0.1, 67; fish unident. 0.1, 0.1, 33. At Wilkes Land (Levick 1914; Penny 1968), Haswell I. (Syrojeckovskij 1966), w. Antarctica (Dombrowski 1925), only euphausiids; other samples w. Antarctica (Murphy) and Ross Sea (Falla 1937), mostly euphausiids, some fish and cephalopods, samples Palmer Land mostly fish, some euphausiids (Eklund 1945).

INTAKE At Terre Adélie, received 0.79 feeds/day during period of greatest growth, 0.53 feeds/day in week before fledging (Ridoux & Offredo 1989). At Signy I., twins had 0.60 feeds/day (n=427), singles 0.65 feeds/day (715) during guard-stage; twins 0.58 feeds/day (24), singles 0.44 feeds/day (215) during crèche-stage (Lishman 1985b). At King George I., each estimated to receive 0.99 meals/day during guard-stage with feeding interval 24.3 h (SE 0.8; Trivelpiece *et al.* 1987). Stomachs at Terre Adélie contained 251 g (163; 30–900; 105) (Ridoux & Offredo 1989). Samples taken before hatching at Davis, 10.9 g; after hatching, 148.1 g. At Signy I., mean size of meals during guard-stage 84.4–163.9 g, crèche-stage 173.1–313.9 g (based on daily weighings); at King George I., chick

stomach contents increase from 436 g to 613 g by 36 days (adult stomach contents = 0.053 chick mass + 0.427, $r=0.36$, $n=41$; Trivelpiece *et al.* 1987); adult stomach contents at same site, Nov.–Feb., 687 g (1313; 492) (Jablonski 1985). Arrivals at nest: 90%, 09:00–18:00, most active period, 15:00–19:00 (Lishman 1985b). Mean daily weight gain Terre Adélie, 70 g (Sapin-Jaloustre & Bourliere 1951); C. Crozier, 91 g (Sladen 1958); C. Roys, 116 g (Taylor & Roberts 1962).

SOCIAL ORGANIZATION Gregarious at breeding colonies and at sea.

BONDS Vary. Mate-retention from one season to next 80% near Casey (Penney 1968), farther S, 18–50% at C. Crozier (Ainley *et al.* 1983) and 56.5% at C. Bird (Davis 1988). Mate-retention probably function of synchronic physiological cycles and fidelity to previous nest-site. Because breeding season farther S is shorter, it may be advantageous to mate with bird arriving at colony about same time rather than wait for mate from previous season. At C. Crozier, slightly higher mate-retention with increasing age (Ainley *et al.* 1983).

BREEDING DISPERSION Colonial. Size of colonies ranges from 20 to >200 000, with 20 000–30 000 common; few with more than 100 000. Colonies made up of discrete sections, each containing a few to several thousand pairs. Nests built far enough apart to make neighbourly pecking difficult. Average distance between central nests 65 cm, peripheral nests 72 cm (Penney 1968). Breeding success lower in nests on periphery of colony than in centre, mainly because great differences between central and peripheral breeders of the youngest ages (Ainley *et al.* 1983). Sites of colonies and nests quite stable.

ROOSTING Usually on ice-floes; land mainly used in breeding season.

SOCIAL BEHAVIOUR Based mainly on observations by Sladen (1958), Penney (1968) and Jouventin (1982). Detailed reviews given by Ainley (1975) and Spurr (1975). Information supplied by K. Green and P.J. Fullagar from detailed field observations. Important components of displays are shape of crown-profile, presence of occipital crest (transverse at back of head); eye posture and exposure of white sclerae; fluffed or sleeked body contour; flipper posture and movements; neck stretching and head-waving. The Eyes Down, a prominent signal. Eyes wide open, exposing the white eyering and gaze turned down to reveal the white sclerae above; component of all major displays. There are several distinctive calls particular to certain displays and often including important information on individual identity (see Voice).

AGONISTIC BEHAVIOUR Both sexes defend territories using pecks and threats (Sladen 1958; Spurr 1975). Often interlock bills with birds from adjacent nests, push and twist and butt breasts (Levick 1914), the loser usually being first to be knocked down (Ainley & Emison 1972; Ainley 1975; Spurr 1975).

Three main **THREAT DISPLAYS** all given with eyes down and crest erect (Fig. 2): **Direct, Fixed One-sided** and **Alternate Stare**: standing or prone bird faces threat ('Glare' of Richdale 1951), flippers held to side, occipital crest raised and eyes rolled downwards. **Direct Stare** (Fig. 3). Given by adults and undefended chicks. Bill pointed at threat (e.g. overflying skua). When neck arched and one side of face presented perpendicular to threat posture termed **Fixed One-sided Stare** (Ainley 1975); usually given before **Alternate Stare** when bird in a crouch arches neck and twists head back and forth to

show one side of face and then other. Alternate Stare accompanied by slow wing-wave. These postures (Fig. 4) usually accompanied by growl call (see Voice) but with decreasing probability of calling in the sequence described. In the **Crouch** (Fig. 5) bird moves back to place centre of gravity over deeply flexed legs, head and neck are withdrawn and bird gapes, pecks or gives Gakker call (see Voice). **FIGHTING (ATTACK)** between conspecifics usually begins with breast thrust forward; birds then bump each other and beat rapidly with flippers, each finally attempting to hold onto other with bill. Fight ends when one of pair falls over, scrambles up and runs away, often through colony with both pursuer and pursued pecked by nesting birds (Fig. 6). Fight may continue elsewhere, or victor may return to nest, and participate in Loud Mutual Display (see below). Attacks common before laying and after re-occupation of site; uncommon between mates, more common among unestablished breeders, with fighting also occurring between chicks. **Charge** (see Spurr 1975), with upright body, raised occipital crest, and bill pointed forwards, is most commonly used against strangers lingering near nest. Also against skuas. Takes the form of few steps or run at offender. **Pecks** are mild form of attack aimed at birds passing occupied nest, or at neighbour; common throughout season, but mostly during nest-building (Sladen 1958). During early courtship, sex-recognition and male's acceptance of female on territory possible through female's **SUBMISSIVE BEHAVIOUR** and smaller size. If female is aggressive, moves quickly or does not bow head, male often pecks her or drives her away. Apparent size of female reduced by more sleeked plumage and lowered head-crest (Ainley 1974).

Behaviours suggesting nervousness (Sladen 1958): (1) When confronted by strange object, bird flicks flipper to-and-fro in jerky fashion. Commonly seen in non-breeders on periphery of colonies. (2) Forehead-feathers raised and occipital crest smoothed. (3) Rapid jerky head-movements seen, for example, when uncertain whether to defend nest or retreat. (4) The call *aark* heard in adults, and more so in nestlings, before entering sea; also heard when bird is being chased. (5) When among nests, birds hold feathers tight against bodies, necks elongated and flippers held back; probably functions to reduce body-size.

SEXUAL BEHAVIOUR Main displays in **PAIR-FORMATION**: Ecstatic and Bill-to-axilla Displays, Bowing and Mutual Displays. **Ecstatic Display**: starts with slow rhythmic flipper beats (slightly less than 2/s) as breast thrust out, neck arched, and with entire body, it is then elongated and pointed upwards. As climax reached, neck and bill stretched to maximum, sides of neck expanded and pattern of throat exposed (Fig. 7), eyes rolled down and backwards, occipital crest raised, flippers still beating horizontally (Fig. 8). Loud distinctive vocalization given with this display, usually a few silent examples before call fully developed (see Voice). After climax, bird relaxes or enters Bill-to-axilla Display. Ecstatic Display common in males, especially lone males at empty nest. Rarely given by females, and then most often by successful breeders after eggs hatch (Ainley 1975). **Bill-to-axilla Display** (Fig. 9): some variation in posture (Penney 1968), but usually bird is standing and leans forwards up to 45°, head rocks and twists from side to side (rotating 50–60°) with bill tucked or directed to either axilla and away from recipient; flippers beat rhythmically backwards and forwards (similar to Ecstatic Display) at high intensity (e.g. following Ecstatic Displays) or may be held motionless in other circumstances. Most often given by males; often in response to Ecstatic Displays of other birds. A dis-

Fig. 2 Crest-erect, Eyes down

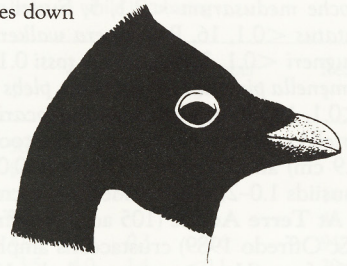


Fig. 3 Direct Stare

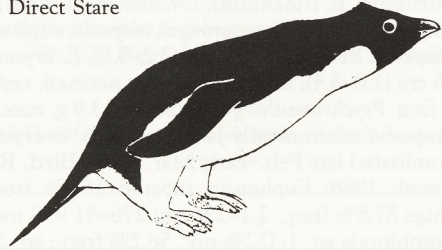


Fig. 4a Fixed One-sided Stare

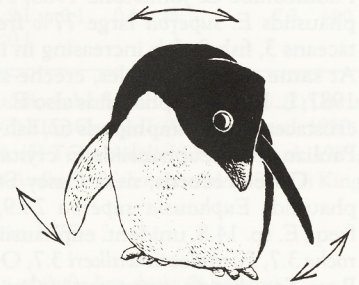


Fig. 4b Alternate Stare

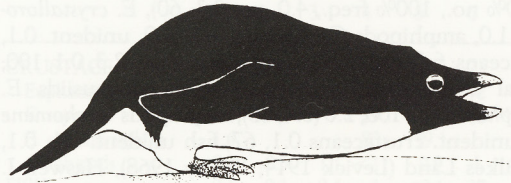
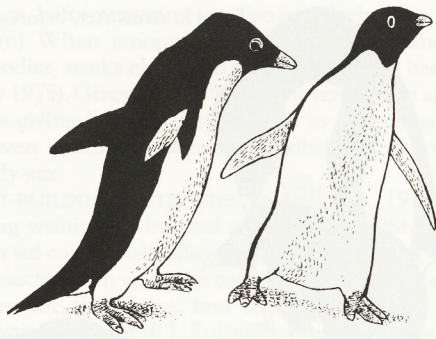
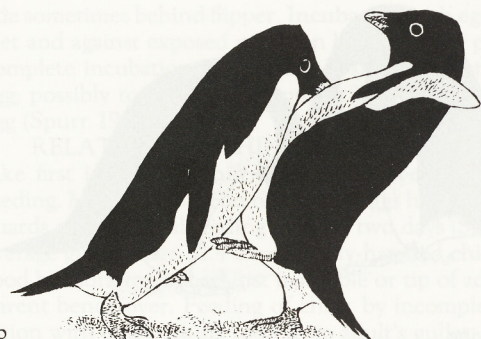


Fig. 5 Crouch

tinctive call (see Voice) is given in time with rocking head (Sladen 1958). Follows Ecstatic Display in 54% of lone males and 86% of incubating or guarding males; rarely performed by females and then usually after hatching (Penney 1968; Ainley 1975). Probably assists pair-formation as threat to other males but not to attracting mate; often given in response to Ecstatic Display of neighbouring birds and given in quick succession with own Ecstatic Display. Also observed after threats towards intruders. Jouventin (1982) identifies display as agonistic signal. **Bowing**: given most commonly by members of pair; head and neck arched forward, bill pointed to ground (Fig. 10); in deep bow, as given by male before copulation, flippers held tightly to sides and slightly forward (see elsewhere). Also seen as female response at nest to male Ec-

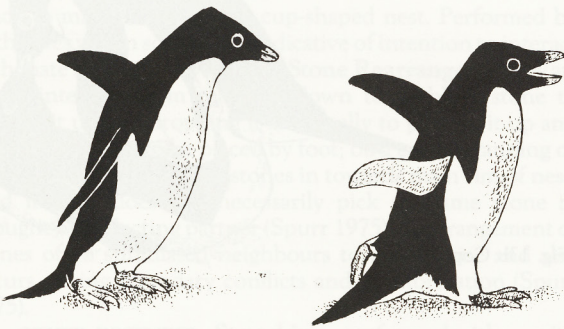


6a



6b

Fig. 6 Fighting



6c

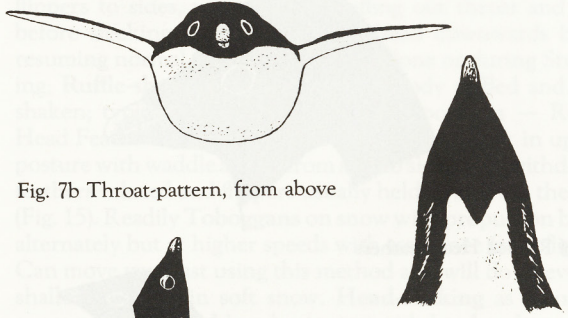


Fig. 7b Throat-pattern, from above

Fig. 7a Throat-pattern

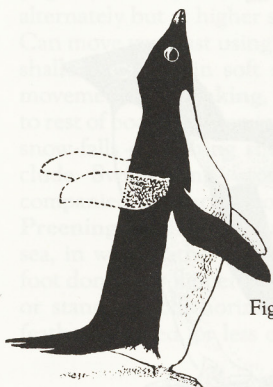


Fig. 8 Ecstatic Display

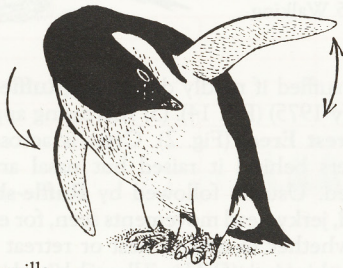


Fig. 9 Bill-to-axilla

static Display. The **Oblique Stare Bow** (Ainley 1975) given by bird in upright posture lowering head to 30-60° below horizontal and presenting one side of face towards bird of opposite sex, with bill closed. Males sometimes have eyes down but not females. The 'crest-erect' is always shown by male but female relaxes or only partially erects crest. Male's bill pointed much more towards the female than her's to him (Ainley 1975). **Loud Mutual Display**, although sometimes given by lone birds, this very common display is usually given by paired birds: the two face each other, bills pointed upwards and open wide, necks stretched out, eyes rolled down and back, occipital crests raised, flippers held to sides (Fig. 11) and heads, necks and sometimes bodies swaying from side to side as distinctive call emitted (see Voice). In other form, **Quiet Mutual Display** (Fig. 12), movements less pronounced, bills closed, and birds either quiet or call softly (a characteristic humming; see Voice). Can be initiated in bird lying in nest by other bird collecting stones. Either form seen after disturbance in colony or in response to Ecstatic Display. Often follows Mutual Bowing. Mutual Display develops in chicks from food begging to outstretched neck and waving head in circular fashion; later modified to sideways head-movement while calls change (see Voice).

Male attracts female to nest with Ecstatic Display. Female responds at nest with Bow followed by Mutual Display. Nest-relief ceremony starts when bird returns from sea and finds nest; immediately gives Loud Mutual Display repeated several times, even if no mate present; mutual Bowing if mate present. If mate on nest, incoming bird settles on egg or chicks, relieved bird stands and stretches. More Loud Mutual Displays occur at lessening intensity, and often a few Quiet Mutual Displays. Relieved bird goes off to collect stones before departing for sea; as each stone dropped Quiet Mutual Display often seen (Sladen 1958). Intensity of display decreases after eggs hatch and chicks grow larger, and stops when chick enters crèche. No allopreening reported (Ainley 1975; Spurr 1975). **COPULATION**. Male is on nest and gives up his place to female; male then Bows deeply and approaches female from side as she lies in nest (**Arms Act** (Fig. 13a); see Spurr 1975). May mount with few preliminary movements or after prolonged period of Bowing. Head bent low, flippers beating, male mounts female half-way along back; female raises bill; vibrates male's bill when brought into contact with female's mandible and chin. Male treading on female's back moves backwards, tail wagging from side to side against female's up-turned tail. Rapid apposition of protruding cloacae as male reaches female's rump (Fig. 13b). Male jumps off, walks round to side of female with head bowed, female flicks tail forwards in jerky movements. Both birds usually shake heads and swallow after copulation. Mounting repeated many times in



Fig. 10 Bowing

Fig. 11a Loud Mutual Display, lone bird

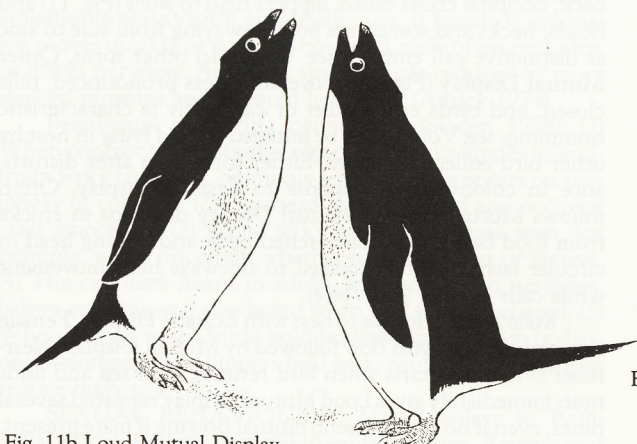
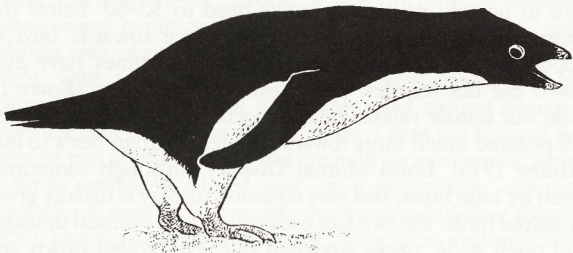
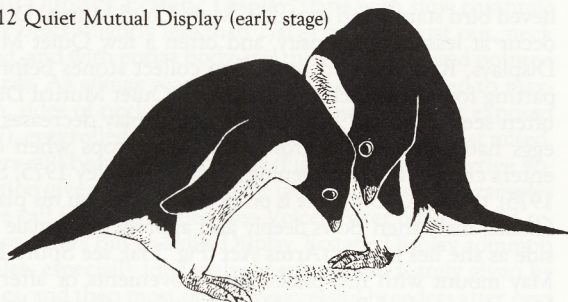


Fig. 11b Loud Mutual Display

Fig. 12 Quiet Mutual Display (early stage)



pre-egg period; coition incomplete in many cases (P.J. Fullagar).

OTHER BEHAVIOURS (Sladen 1958; Ainley 1975), suggesting nervousness. (1) When confronted by strange object, bird flicks flipper to-and-fro in jerky fashion (termed **Slow-wing-flap** by Ainley 1975). Commonly seen early in breeding season, often away from the colony and in non-breeders on periphery of colonies. (2) Feathers of forehead and occipital-

Fig. 13a Arms Act, before copulation



Fig. 13b Copulation



Fig. 14 Ruffled Head-feathers

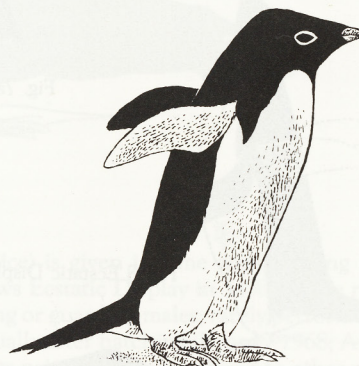


Fig. 15 Walking

crest ruffled if mildly disturbed (**Ruffled Head Feathers** of Ainley 1975) (Fig. 14). (3) Increasing apprehension indicated by **Crest Erect** (Fig. 2). Crest is across back of head with feathers behind it raised but nasal and forehead feathers sleeked. Usually followed by **Ruffle-shake** (see below). (4) Rapid, jerky head movements seen, for example, when uncertain whether to defend nest or retreat (see **Stare**, **Alternate Stare**, this text). (5) The call *aark* heard in adults, and more so

in nestlings, before entering sea; also heard when bird is being chased. (6) When among nests, birds hold feathers tight against bodies, necks elongated and flippers held back (**Sleek** of Ainley 1975). Given before fleeing; by females on approaching males giving Ecstatic Displays and by birds stealing nest stones, even in absence of owner. Probably functions to reduce body-size.

NEST-BUILDING ACTIVITIES (see Spurr 1975). **Stone Searching** within and beyond area of colony. Stones sometimes carried considerable distances (20 m). Stealing common. Stones selected with apparent care. Choice often rejected and exchanged for alternative; first choice not usually rejected until substitute found (P.J. Fullagar). **Nest-scraping**: bird lying in nest-scraps kicks out of bowl with backwards motion of one foot; usually shifting stones towards the rim. Process tends to maintain a circular cup-shaped nest. Performed by both sexes and in some cases indicative of intention to interact with mate (e.g. see Copulation). **Stone Rearrangement**. Varies in intensity from reaching down to nibble a stone to picking it up and dropping it and finally to picking it up and carrying it round to be placed by foot; bird can be standing or lying down. Process drags stones in towards main rim of nest. Bird in nest does not necessarily pick up same stone as brought by collecting partner (Spurr 1975). Rearrangement of stones often stimulated neighbours to do likewise and also occurs during boundary conflicts and pair-formation (Spurr 1975).

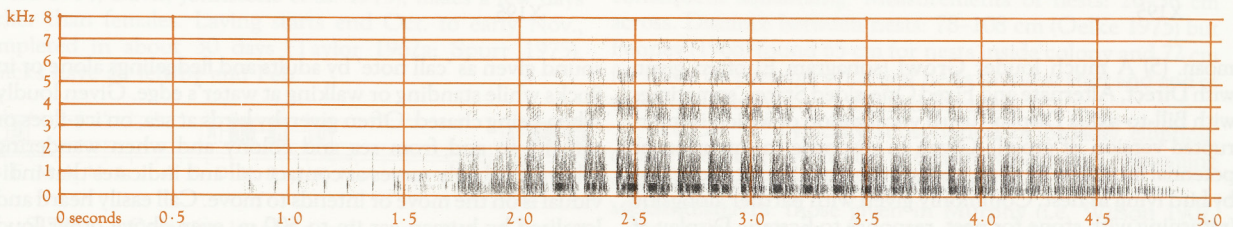
OTHER POSTURES: **Stretching**, performed either with flippers held backwards and body arching forwards with yawning or by rising to full height, lifting head up, pressing flippers to sides, yawning and puffing out throat and neck before sleeking whole body from head downwards before resuming normal posture. **Yawning** alone or during Stretching; **Ruffle-shake**, feathers of entire body ruffled and body shaken; typically follows apprehensive postures — Ruffled Head Feathers and Crest Erect (see earlier). Walk in upright posture with waddle action from side to side, neck withdrawn, feathers relaxed and flippers usually held away from the body (Fig. 15). Readily **Toboggans** on snow with propulsion by feet alternately but at higher speeds with assistance from flippers. Can move very fast using this method and will do so even up shallow inclines in soft snow. **Head-shaking** as a comfort movement and **Shaking**, beginning with head and spreading to rest of body and seen in birds coming out of water or during snow-falls or drifting snow. Other comfort movements include **Swallowing** usually after Head-shaking; and accompanied by rasping sound from rubbing lamellae of bill. **Preening** usually occurs after coming ashore, before going to sea, in wet weather or during thaw. **Head-scratching** with foot done over flipper. When **Sleeping**, birds either lie down or stand up, bill horizontal, head withdrawn to shoulders, feathers relaxed, or less often, stand with bill tucked to one

side sometimes behind flipper. **Incubation** with eggs between feet and against exposed patch on belly in lying posture. Incomplete incubation in standing posture suggested for first egg; possibly to retard development before laying of second egg (Spurr 1975).

RELATIONS WITHIN FAMILY GROUP Males take first incubation shift lasting two weeks; female at sea feeding. Male or female on nest when eggs hatch. Each parent guards chicks; usual feeding interval two days (Sladen 1958), average guard-stage 22.4 days. Newly-hatched chick begs for food by vibrating bill against mandible or tip of adult's bill as parent bends over. Feeding of chick by incomplete regurgitation with chick taking food from adult's gullet. Feeding by non-breeders recorded by Crawford (1974). Parents give Loud Mutual Displays with accompanying calls whenever return to nest; chicks in crèche recognize parent's voice and come to it. Crèches build slowly from small groups that coalesce. Feeding chases ensure chick fed away from others; after feeding, parent wards off chick with series of pecks. At fledging, chicks go to sea independent of parents (Penney 1968).

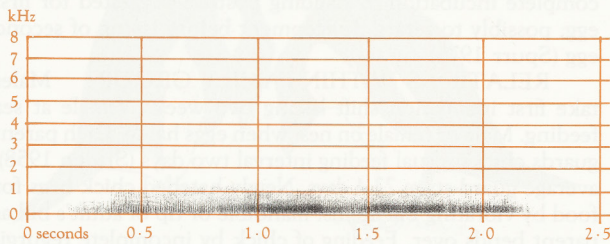
VOICE Most extensive studies by Penney (1968) and Jouventin (1982), both with sonagrams. Further information reviewed by Ainley (1975) and Spurr (1975). This account based on field observations and recordings by P.J. Fullagar at Whitney Pt, Casey, in late 1989. Most conspicuous calls are rhythmic throbbing sounds associated with Ecstatic Display and Loud Mutual Display. No calls sexually diagnostic but some rarely given by female. Important individual differences first reported by Penney (1968) and subsequently confirmed (see Ainley 1975). No regional variation. Non-vocal sounds include (1) dropping stones during nest building; (2) loud beating of flippers against opponent during fighting; (3) rustling sound caused by rasping of bill plates and tongue during bill-cleaning comfort movements; (4) an almost inaudible tapping of bills during copulation; (5) treading sounds of male stomping on the back of female during copulation.

ADULT (1) Call associated with full Ecstatic Display starts with soft rhythmic pumping sounds (not at same rate as flipper beats), breast heaving with each of the deep staccato *thumps*; call then bursts into climax of pulsating hoarse series of rasps (sonagram A). Rate of pre-climax pumps at about 7.4 pulses/s (7–7.7) for about 5.3 s (3.2–6.9). Energy centred a little under 500 Hz then followed by loud, more clearly structured rasping pulses continuing for about 3 s (1.9–4.3) with much greater emphasis at the lower frequencies and strong harmonic structure (Penney 1968). Bill only slightly open during this call except at most 'imploring' level, at highest excitement, when it is clearly open. Rendered *dood-dood-dood-dood . . . arr-rar-rat-rar-raah*. (2) Call with Bill-to-Axilla Display is wheezy interrupted growl sounding like moaning expiration of breath with emphasis on second syllable of each pair. Ren-



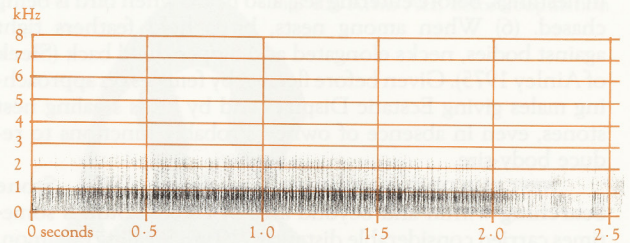
A P.J. Fullagar; Whitney Pt, Casey, E. Antarctica, Nov. 1989; X195

dered as *oo-ah...oo-ah...oo-ah...* (sonagram B). Length of call varies from 0.3–4.1 s with 3 to 8 pulses synchronic with each

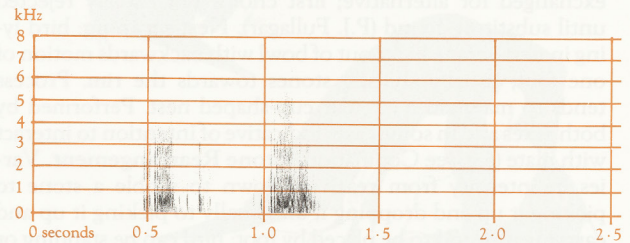


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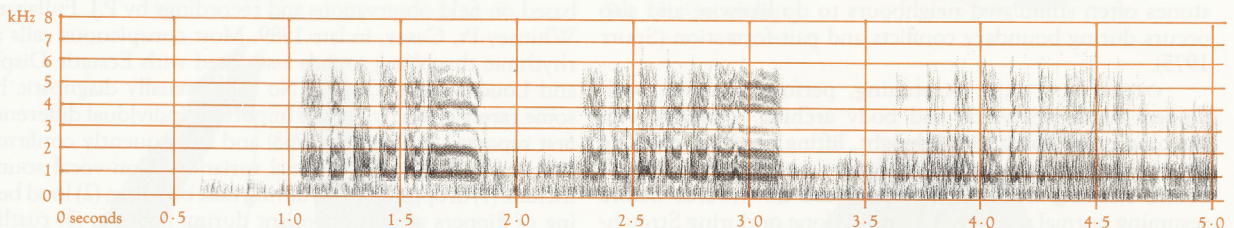
swing of head. Most energy below 1 kHz (Penney 1968). (3) Call given during Loud Mutual Display is well described as trumpeting (Ainley 1975). Can be uttered by single bird or most commonly in duet with partner after pair-formation. Not given by unpaired birds. A harsh loud pulsating call with prolonged ending. Rendered as *ug-gug-gug-gug-gaah*; with emphasis on last syllable. A sonorous call uttered with bill open (sonagram C). Structurally similar to the Ecstatic Display



E P.J. Fullagar; Whitney Pt, Casey, E. Antarctica, Jan. 1990; Y1



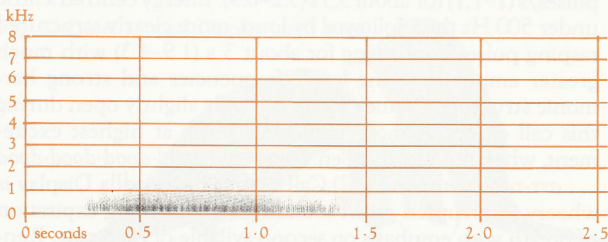
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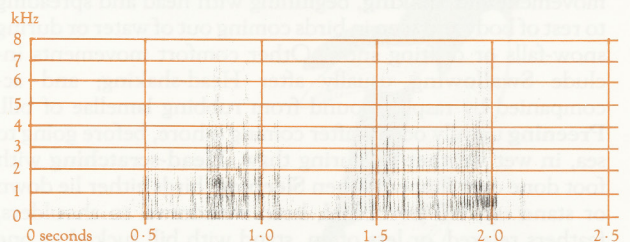
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call. Repeated in sequence with decreasing intensity following initial most explosive outburst. Decreasing complexity as amplitude declines. Pulsating phrases conclude with drawn out slurred version. Highly characteristic of individual (Penney 1968). Incubating adults reported to give this call at time of hatching (Ainley 1975). (4) A slow humming sound given during Quiet Mutual Display (sonagram D) best described as soft

lished pair-bond (Penney 1968). Call grades into **Attack** vocalization (sonagram F), which is sharp squawk in form of abbreviated harsh and loud growl given at moment of lunging; and the **Gakker** vocalization given by intensely irritated birds (sonagram G). A rattling growl like a deep scolding grunt *gwa-a-a-a-a-a*, or *gwarrr* or *grrrr* (Sladen ex Ainley 1975). (6) **Contact Call: Aark** vocalization (sonagram H): sharp barking



D P.J. Fullagar; Whitney Pt, Casey, E. Antarctica, Nov. 1989; X195

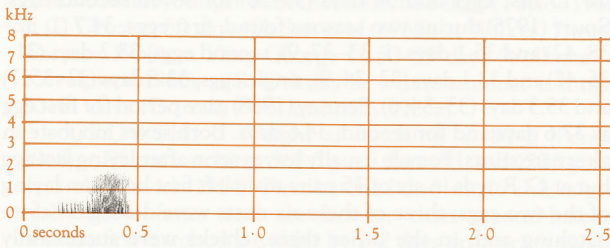


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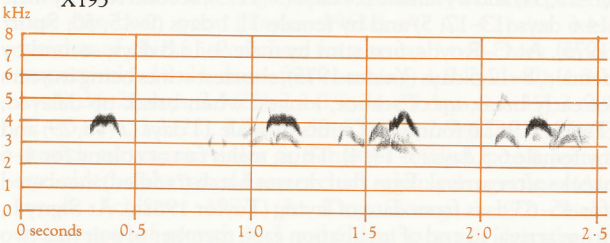
moan. (5) A much louder **Growl** (sonagram E) often given with Direct, Alternate and Fixed One-sided Stares, sometimes with Bill-to-axilla Display (usual vocalization of which is interrupted version of growl). Given in response to intrusion or potential intrusion by skua, penguin or man. Sometimes given by bird lying in nest. Commonly given with partner alongside (returning with stone for nest, response to Ecstatic Display of partner, pair re-uniting after brief separation, response to Loud Mutual Display by partner). Functions to ensure estab-

sound given as 'call note' by adults and fledgelings alone or in flocks while standing or walking at water's edge. Given loudly when being chased. Often given by birds at sea, on ice-floes or moving to and from sea and colony and when wandering ashore. Probably serves as contact call and indicates that individual is on the move or intends to move. Call easily heard and localized by human ear up to 500 m, even above other loud noises (Ainley 1975).

YOUNG Brief *peeps* on hatching. Readily audible at



H P.J. Fullagar; Whitney Pt, Casey, E. Antarctica, Nov. 1989; X195

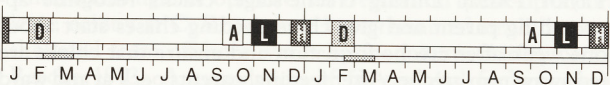


I P.J. Fullagar; Whitney Pt, Casey, E. Antarctica, Jan. 1990; Y1

colonies. Small chicks give weak repeated *peeps* (sonagram I). Call acquires wavering quality by 3 weeks of age (late guard-stage) with falling pitch. Recognition of parents by chick (from characteristics of Loud Mutual Call) well demonstrated by Penney (1968). Call of young becomes like that of Loud Mutual Display call but more highly pitched. Further development of adult calls, during maturation of young, not studied.

BREEDING Well known. Most important studies: Signy I. (Sladen 1958); Hope Bay (Sladen 1958); Wilkes (Penney 1968); Pte Géologie (Mougin 1968); Port Martin (Sapin-Jaloustre 1960); C. Adare (Levick 1914); C. Hallett (Reid 1964, 1965); C. Bird (Spurr 1975); C. Crozier (Sladen *et al.* 1968; Le Resche & Sladen 1970; Ainley & Schlatter 1972; Ainley *et al.* 1983); C. Royds (Taylor 1962a; Stonehouse 1963; Yeates 1968). Breed colonially, often in vast numbers (10^6) on hill-sides and coastal flats free of late-lying snow; sometimes associated with other penguins.

SEASON Oct.–Feb., well synchronized, but earlier in n. than s. colonies (Sladen 1958; Lishman 1985a) and earlier in favourable than in unfavourable seasons at same colony (Spurr 1975). Breeding earlier than expected in Ross Sea at s. limit of range either to ensure enough time for completion of breeding cycle or because sea-ice breaks up early in those latitudes (Stonehouse 1963, 1966; Ainley & LeResche 1973). Birds arrive at colonies from late Sept. (Signy I., Lishman 1985a; Hope Bay, Ross I., Sladen 1958) to mid-Oct. (S. Orkneys, Valette 1906; Petermann Is, Gain 1914; C. Adare, Levick 1914; Davis, Johnstone *et al.* 1973); males a few days earlier than females. Laying starts end Oct. to early Nov., completed in about 30 days (Taylor 1962a; Spurr 1975). Chicks have all left by end Feb.



SITE Colonies in areas well exposed to sun and often to wind, especially in high latitudes, so that they are kept

free from snow drifts (Tenaza 1971; Muller-Schwarze & Muller-Schwarze 1975; Yeates 1975; Murphy); egg losses do not occur at C. Crozier until wind speed >200 km/h (Ainley & LeResche 1973). At some locations, sheltered nest-sites possibly favoured; report from C. Royds of nesting areas shifting to more sheltered locations from 1911–46 (Taylor 1962a). At lower latitudes, snow drifts do not affect breeding success and exposed sites not favoured (Volkman & Trivelpiece 1981). On rocky and pebbly places on flat or irregular terrain formed by beaches and talus, or on hill-slopes, even as high as 300 m asl (C. Adare; Wilson 1907; Levick 1914). On King George I., 94.8% pairs nested on moraines on lava flows, 3.9% on low pebble ridges parallel to shore, and 1.2% on raised terraces and cliffs ($n=32\ 918$; Jablonski 1984). Breeding distribution limited by availability of ice-free land (Caughley 1980; Jablonski 1984), access to open water near pack-ice for feeding (Stonehouse 1963; Ainley & LeResche 1973; Spurr 1975; Yeates 1975; Caughley 1980; Lishman 1985b), steepness of slopes, and character of surface (Jablonski 1984). At King George I., nest at higher levels than other pygoscelid penguins; 13.8% of birds at 1–10 m asl, 1.2% at 11–20 m asl, 40.0% at 21–30 m asl, and 45.0% at 35–40 m asl. Use mainly flat or gently sloping surfaces; mean (\pm SE) slope at colony sites $5.7 \pm 0.4^\circ$ (Volkman & Trivelpiece 1981), maximum slope $40\text{--}50^\circ$ (Jablonski 1984); mean (\pm SE) distance from landing beach 131 ± 4.3 m (Volkman & Trivelpiece 1981). Largest colonies where dispersal of fast sea-ice occurs early in breeding season, and birds can feed in open water close to colonies (Stonehouse 1963). When birds first arrive, nearest open water may be 32–60, even 100 km, distant (Sladen 1958; Taylor 1962a). Nests on ground, usually most crowded on knolls but just out of reach of pecking by neighbouring birds. Islets in frozen ponds within area of colony avoided unless islet is connected by causeway to higher ground (Murphy).

NEST, MATERIALS A scoop or hollow, surrounded and lined with pebbles up to the size of an egg and mostly well rounded; bones occasionally used. Nests on low ground threatened by melt-water may be built higher by addition of stones (Murphy). Nests usually built after thaw, though well-made nest reported on 30 cm of snow (Sladen 1958). Andersson (1908) and Murray (1909) originally recorded that males select site and start building before females arrive. Wilson (1907) and Levick (1914) 'proved', according to Murphy, that females select sites before mating. Falla (1937), Taylor (1962a) and most recent accounts, however, show that males are initiators. Both sexes build; before pairing by male; later both birds take turns, one lying on nest and arranging stones collected and dropped on nest by its mate. Additions made by both birds between nest-relief and relieved bird returning to sea; usually collected near nest but, if carried into colony for some distance (<100 m), dropped within 2–3 m of nest in ecstasy of display (Taylor 1962a). Much pilfering of stones from neighbouring or unoccupied nests, with consequent squabbling. Measurements of nests: 26–36 cm across. Distance between nests: 78–108 cm (Oelke 1975) but Penney (1968) found 65 cm for nests inside colony and 72 cm for those on periphery. Largest nests found at start and end of season, made by non- or failed breeders.

EGGS Typically subspherical or broadly elliptical; chalky surface; white or greenish when laid, becoming stained, with green inside shell (Murphy).

MEASUREMENTS: those given in Murphy (i.e. Wilson 1907, $n=96$: 64–72 x 50–55; av. weight 129 g; Gain 1914, $n=c.$ 50; 61–77.5 x 47–59.5; weight 75–148 g) do not recognize great

differences between first, second and third eggs. Taylor (1962a) distinguishes thus:

1st (n=32): 69.8 (70.4–73.6) x 55.8 (52.5–60.2); weight 124 (105–145)

2nd (n=21): 68.7 (70.0–72.3) x 54.5 (48.1–58.1); weight 115 (90–135)

3rd (n=12): 66.1 (63.4–71.0) x 51.4 (44.5–55.0); weight 101 (70–125)

Singles (n=10): 69.2 (65.4–74.3) x 54.1 (49.5–57.5); weight 117 (95–130).

See also Clarke (1906), Mougin (1968), Yeates (1968), Lishman (1985a).

CLUTCH-SIZE Normally 2. At C. Royds, 19 x C/1 (6 of 57 clutches laid before 19 Nov., 13 of 43 laid later), 81 x C/2. C/3 very rare and only four noted in routine work outside sample area. Single eggs mostly laid by birds breeding for first time, smaller than first eggs in larger clutches (Taylor 1962a). At C. Bird colony, clutches in central nests (at least one territory between nest and colony edge) had 1.89 eggs (0.10; 197); peripheral nests (exposed at colony edge) 1.78 eggs (0.17; 390); F Test, $P < 0.01$; clutches in isolated nests (no boundary contiguous with other territories) averaged 1.45 eggs (0.25; 11). Clutches laid after 20 Nov. had more single eggs and lower average than earlier clutches (Spurr 1975). Murphy claimed replacement laying after loss but at C. Royds females left for sea immediately after full clutch laid and did not return for about 2 weeks. Thus, replacement laying could occur only several weeks after loss and, in view of short laying period, second clutches most unlikely (Taylor 1962a; Sladen 1958). When first eggs (n=19) removed immediately after laying, second and third eggs laid in 12 nests, only second eggs laid in three nests and other four nests were deserted. When first egg lost naturally within 24 h of laying (n=6), two more eggs in four nests and only one more in two nests were laid (Taylor 1962a). Eggs that roll out of nests are not retrieved (Penney 1968) but may be incubated by non-breeders (LeResche & Sladen 1970).

LAYING At C. Royds, synchronized between 4 Nov. and 4 Dec. (Taylor 1962a). Starts about 12 days after arrival of first birds. At C. Bird, mean dates of laying of first egg in two seasons, 11 and 13 Nov. each ± 4 days; of second eggs (n=652) in four seasons, 14, 15, 16, 17 Nov. all ± 3 –4 days (Spurr 1975). Annual variation in laying dates of marked individuals smaller than range of dates in whole population; some females laid consistently near mean date of laying; others consistently early or late (Spurr 1975). Lishman (1985a) gave date of first eggs as 6–10 days after females arrive. At C. Royds, interval between first and second eggs (n=105), 14 x 48 h, 71 x 72 h, 20 x 96 h, all ± 24 h; between second and third eggs, 72 h in 17 nests (Taylor 1962a). Sapin-Jaloustre & Bourliere (1951) record one interval of 120 h. Lishman (1985a) found 72 h.

INCUBATION Eggs may be incubated on top of feet (Mawson 1915) and inner egg at least seems always to rest on the feet (Menegaux 1907). Starts fully only with completion of clutch, first egg being merely covered till then. In 56 of 57 nests in which two eggs hatched, first egg hatched 1.44 days (0–5; Taylor 1962a) and 1.43 days (0–3; Spurr 1975) before second, which indicated equivalent of 34 h of continuous incubation in interval of c. 3 days between layings. **INCUBATION PERIOD:** at C. Royds, average 34.1 days (1; 150) from day of laying to day of final emergence of chick; from laying to hatching of last egg, 33.3 days (30–37; 78; Taylor 1962a). Levick (1914) gave 37 days for one first egg, 31 and 33 days for two second eggs. Sladen (1958) gave average 36 days (35–38)

for 13 first eggs and 34 days (33–36) for seven second eggs. Spurr (1975) during two seasons found: first eggs, 34.7 (1; 32–38; 42) and 35.1 days (1; 33–37; 9); second eggs, 33.2 days (31–35; 42) and 33.1 days (32–34; 9); single eggs, 33.8 days (32–35; 7) and 35.3 days (33–34; 6). Penney (1968) gave period for first egg as 37.6 days and for second, 34.6 days. Both sexes incubate in alternate stints. Female usually leaves soon after laying last egg but at C. Royds in six of 35 pairs male left first between laying of the two eggs; three of these six nests were deserted before hatching and, in the other three, chicks were successfully reared (Taylor 1962a). At C. Bird, first stint by male 14.8 days (7–23; 54) and by female 6.4 days (3–11; 5); second stint by male 14.6 days (13–17; 5) and by female 11.1 days (9–15; 50; Spurr 1975). At C. Royds, first stint by male 9–13.8 days; second by female, 8–12.5 days (Yeates 1975), shortest stints being in years of early break-up of sea-ice, longest when break up delayed; Taylor (1962a) found first stints by male 11 days (7–18; 29) and by female 6.5 days (3–14; 4). Thus, males fast at colony for 4–6 weeks after arrival. Eggs that do not hatch (?added) incubated for 45–63 days from date of laying (Taylor 1962a). At Signy I., from arrival to end of incubation each member of pair had two stints of fasting (Sladen 1958) but at C. Royds each bird had shorter and more frequent spells at sea during same period (Taylor 1962a).

YOUNG Semi-altricial, semi-nidicolous. Hatching takes 24–48 h after first chipping (Sladen 1958); nine chicks took less than 24 h to hatch, 38 took 24–48 h, three took more than 48 h (Taylor 1962a). Some chicks are not fed for up to 3 days from hatching, slowly losing weight and doubtless surviving by absorbing yolk-sac, till it is totally absorbed when about 1 week old (Taylor 1962a). Hatched with uniform sooty protoptile but some chicks have pale-grey or silvery-white down and blackish heads (Sladen 1958; Murphy); at C. Royds all intermediates noted between these two extremes of dimorphism (Taylor 1962a). Mesoptile of dark-grey, thicker, woolly down acquired by 10 days old and starts to be shed at 20–25 days old, little remaining after 45–50 days old, though some may persist to departure (Taylor 1962a). Young attended by both parents alternately during guard-stage of about 1 month at Hope Bay and Signy I. (Sladen 1953) but at C. Royds for only 22.4 days (17–24; 122), with two-thirds being first left unguarded 20–24 days after hatching; early chicks guarded for longer than later ones so that, though hatching in colony is spread over 4 weeks, 90% of chicks enter crèches within 2 weeks; earlier crècheing by late chicks more noticeable inside colony than on periphery or in isolated nests (Taylor 1962a). Single chicks guarded for 2.4–5.7 days longer than first or second chicks (Lishman 1985a). During guard-stage parents usually exchange duties every day or twice in three days; absences by one bird of up to 4 days rare (Taylor 1962a). Crèches build up slowly by coalescence of small groups of chicks that have assembled, perhaps guarded by a few adults (Murphy). The crèche-stage completes the period of fledging. Both parents feed only their own chicks, even during crèche-stage, by incomplete regurgitation. Very young chicks may be fed several times during attendance of any one parent at nest; when older, chicks fed soon after arrival of parent (Sladen 1958; Taylor 1962a). During crèche-stage, chicks recognize approaching parent and give chase; feeding chases start about one week after crèche formation and ensure that chicks are fed away from crèche. After feeding, parents peck at and ward off chicks. Non-breeders have been known to feed chicks (Crawford 1974). Period of rearing: at C. Royds, mean age of departure 50.6 days (41–56; 113); late-hatched young tended

to leave when younger than those hatched early (Taylor 1962); at C. Crozier, 50 days (Sladen *et al.* 1968); at Wilkes, 7 weeks (Penney 1968); at King George I., 50–55 days (Volkman & Trivelpiece 1980); at S. Orkney Is, where summer is longer, 60–61 days (Croxall 1985; Lishman 1985a).

GROWTH Weight at hatching: c. 80 g (Penney 1968); c. 85 g at hatching, 368.5 g at 5 days old, and 1205 g at 12 days old (Levick 1914). First-hatched and single chicks generally grow faster and are heavier than second-hatched because first-hatched are older by 1–2 days on average and get greater share of food. Survivor of two chicks also grows more slowly than first and single chicks, probably because parental care has been poor (Taylor 1962a). At C. Crozier, mean weights of chicks in crèches, for one- and two-chick broods respectively: 18–21 days after hatching, 1.8 kg (n=7), 1.3 kg (n=4); 26–29 days, 2.5 (23), 2.3 (15); 34–37 days, 3.1 (35), 2.6 (9); 42–45 days, 3.2 (22), 3.2 (10); 50–53 days, 2.9 (62), 2.7 (34) (for growth curves see Ainley & Schlatter 1972). Up to 6 years of age, older adults raised heavier chicks than younger ones (Ainley & Schlatter 1972). At King George I. (91 chicks), increments of growth in 3 and 6 days intervals described by logistic equation with constant = 0.146 and asymptotic weight = 3.940 kg; feet and flippers grew more rapidly than bills; growth slow for first 5 days, then linear till 36 days; after reaching maximum weight (74% av. ad. wt.), weight decrease to 70% av. ad. wt. at 52 days; no differences in rates of growth of chicks of different categories (Volkman & Trivelpiece 1980).

FLEDGING TO MATURITY At C. Royds, crèches began to break up, change or amalgamate by 22 Jan., but first actual departure on 30 Jan. Many individuals leave gradually, gathering near the shore, making short swims and returning to colonies for 2–3 days. Chicks fed by parents to within a day or so of leaving but then are not importunate for food. Some chicks, however, leave shore immediately and swim right away (Sladen 1958; Taylor 1962a). Period of departure at C. Royds, 30 Jan. to 25 Feb. Chicks independent of parents from departure. Age at first breeding: females 3 years (7%), 4 years (33.3%), 5 years (25.3%), 6 years (25.3%); males, 4 years (3.9%), 5 years (18.2%), 6 years (32.5%), 7 years (42.6%) (Ainley *et al.* 1983). Return to natal colonies at 2–3 years old (Volkman *et al.* 1982).

SUCCESS Fluctuations in timing and success of breeding reflect varying food supply, which depends on complex ice/ocean/atmosphere interaction (Sladen 1958). Breeding success correlated with euphausiid abundance over continental-shelf water (Whitehead *et al.* in press); reduced breeding success in years when fast-ice persists may occur because sea-ice affects abundance and distribution of prey (Whitehead *et al.* in press) or because travelling across ice to feeding grounds is energetically costly (Ainley & LeResche 1973; Yeates 1975; Lishman 1985b). Birds in colonies in Prydz Bay rely on counter-flowing coastal and offshore wind-systems to drive circulation, upwelling and mixing of waters (Whitehead *et al.* in press). At C. Crozier, breeding success higher in years with strong offshore winds (up to 160–190 km/h), which break up sea-ice and move it out from coast; when winds light or onshore, sea freezes and break-up occurs later; colony at C. Royds may have remained small because sheltered from offshore winds by mountains (Ainley & LeResche 1973). Accumulation of fat essential for successful breeding. Generally only first-hatched chick from first-laid egg fledges. Older birds raise heaviest chicks at fledging. First-time breeders have 25% infertility and lose 0.3–0.4 eggs/nest

on average; later, lose only 0.1–0.2 eggs/nest and 6–7 years old birds have only 13% infertility (Ainley 1975; Croxall 1985). At C. Royds in 1959–60; 225 eggs laid (in 122 nests); 150 (66%) hatched, 22 (10%) failed to hatch and 53 (24%) lost; 113 chicks (75% of hatchlings) fledged; total success 50% or, estimated from whole colony, about one chick per pair. Highest success (c. 55%) in early nests inside colony; lowest, (c. 28%) in late peripheral nests; success of late central nests, c. 45%, and of early peripheral, c. 52% or intermediate (Taylor 1962a). At C. Bird, success of C/2s was 0.50–1.68 chicks reared per pair and significantly better than that of C/1s with 0.16–0.43 chicks reared per pair in all comparisons of dates of laying and position in colony of nests. Most losses during first two weeks of incubation by predation by skuas or loss of one adult. Success of individual breeders did not change significantly if individual stayed as central or peripheral breeder in successive seasons but was better if status changed from peripheral to central or vice versa. No change of success if change of mates occurred, provided eggs actually produced, but change of mates often led to non-laying (24.7% males; 28.4% females). Number of birds that, having bred one year, returned the next increased from c. 65% to c. 80% over three seasons, as did percentage that bred again. Total success varied from 42.8 to 65.9%, averaging 57.3% for four seasons (1967–71) (Spurr 1975). At C. Royds over four seasons, loss of eggs 12–63%, loss of chicks 10–28%; lowest losses in years of early break-up of sea-ice, highest when break-up late (Yeates 1975). Survival to crèche-stage at Admiralty Bay, 1.02 chicks per pair (Volkman *et al.* 1982). Mean survival to that stage at Davis over seven seasons (1981–88) 0.95 (0.67–1.4) chicks per pair; three worst years when *Euphausia superba* or amphipods were main food after hatching and pack-ice extensive; four best years when *E. crystallorophias* was main food and pack-ice less dense (Whitehead *et al.* in press). At C. Crozier, survival to fledging 0.64–0.92 chicks/pair (Oelke 1975). At Signy I., total success in four seasons: 38.5, 7.5, 76.7 and 22.4% (Lishman 1985a). **LOSSES, PREDATION.** In S. Shetland Is, loss of eggs mostly by desertion before return of mate (Trivelpiece *et al.* 1983). At C. Royds and C. Bird, mostly by competition for nest-sites, desertion, building of inadequate nests and improper incubation; predation by skuas not important (Taylor 1962a; Spurr 1975). Chicks are mostly lost to skuas: 67% of all losses at C. Royds (Taylor 1962a); 45% at C. Bird (Spurr 1975); only other important losses caused by desertion by, or loss, of adult and by exposure. Sheathbills *Chionis alba* recorded as predator at Hope Bay and Signy I. (Sladen 1958). At Ross I., 18.3% of eggs laid and 23.2% of chicks taken by skuas, 15.3% of eggs lost by desertion and 12.9% of chicks by starvation; mostly in peripheral nests (Davis & McCaffrey 1986). At Davis, Southern Giant-Petrels *Macronectes giganteus* cast up boluses containing mostly remains of Adelie Penguins, probably from carrion (Green 1986).

PLUMAGES

ADULT Definitive basic. Assumed at beginning of second year, but age of first breeding 3 to 8 years (Ainley 1975). **HEAD AND NECK.** White eye-ring partially formed by minute white feathers. Head and upper throat, black with silvery blue wash (appearing less blue than any other penguin). Feathers black-brown, merging to concealed white bases. Small blue-grey (88) central tip, distal half of rachis black (89), proximal half of rachis white with black (89) central stripe. **UPPERPARTS** as for head and upper throat; black with silvery blue wash. Upper tail-coverts, pale grey (86) with black (89)

rachis. TAIL, black (82), fades to dark brownish grey (c79). UPPERFLIPPER. Upperside blackish (82) with white trailing-edge from elbow to near tip. UNDERPARTS and lower throat white, save for small blackish (82) wedge at base of flipper. White extends farther forwards at sides of throat than in centre. UNDERFLIPPER. Underside white, with blackish (82) leading-edge and tip, and very narrow black (82) edging to elbow.

DOWNY YOUNG Protoptile silvery grey (c85) with greyish (brownish 84) chin and throat, and sooty-brown crown and hindneck. Mesoptile assumed after 10 days; dark brownish-grey with slightly lighter underparts.

JUVENILE Lacks white eye-ring. Chin and upper throat, white or pale greyish (-). Upperparts slightly more blue-grey than adults.

ABERRANT PLUMAGES Isabelline, albino and melanistic individuals, and albino downy young, known (Falla 1937; photos in Lindsey 1986).

BARE PARTS Based on Bierman & Voous (1950), skins (MV) and photos in Lindsey (1986) and Peterson (1979).

ADULT Iris, black-brown. Eye-ring and eyelids, white. Bill black (82) with orange latericorn, narrow orange base to lower mandible, and varying amount of orange at bill tip and on underside of lower mandible. Some individuals with black (82) underside to lower mandible, and tomlia of upper mandible. Tarsus and upper surface of feet, pinkish white to flesh-pink (c3), sometimes with blackish (82) tips to toes and webs. Soles and claws, black (82).

DOWNY YOUNG Bill, black (82).

JUVENILE As adults, but lack white eye-ring. Eyelids, grey (-).

MOULTS Based on Penney (1967) except where stated. Takes place on sea-ice and less often on land; numbers moulting on land vary annually, depending on ice-conditions (Sladen 1958). New feathers first visible in central breast and back. Old feathers remain longest on crown, foreneck, sides of neck and legs.

ADULT POST-BREEDING Definitive pre-basis. Duration ashore 19.8 days (15-25; 45). First adults come ashore first week Feb.; numbers peak in first week Mar.; last adults leave in first week Apr. Mean dates of coming ashore: successful breeders 3 Mar. (17 Feb.-10 Mar.; 25), unsuccessful breeders 1 Mar. (25 Feb.-6 Mar.; 8). Half of presumed non-breeders begin moult before 19 Feb. Average time at sea before moult 9 days (1-15) in 10 successful breeders, 46 days (41-51) after loss of eggs or chicks in three unsuccessful breeders (Taylor 1962a).

POST-JUVENILE Come ashore to moult in late Jan. and early Feb., often with missing rectrices. Time ashore 18.6 days (15-21; 12).

MEASUREMENTS (1) C. Crozier, recently killed birds; FLIPPER(D) = length by dissection, BILL(G) from gape to tip, BILL W = bill width at gape, TARSUS(D) = length by dissection (Ainley & Emison 1972). (2) Several locations, skins;

| | | | | |
|-----------|-----|-----------------------|-----------------------|----|
| BILL(G) | (1) | 62.2 (2.3; 58-67; 31) | 59.7 (2.8; 55-67; 18) | ** |
| BILL W | (1) | 32.7 (1.6; 31-38; 31) | 31.2 (1.5; 29-34; 18) | ** |
| TARSUS | (2) | 31.1 (1.69; 30-34; 8) | 30.5 (1.26; 29-33; 6) | * |
| TARSUS(D) | (1) | 32.8 (0.9; 31-34; 23) | 32.2 (1.2; 30-34; 13) | * |
| TOE | (2) | 72.5 (4.07; 66-80; 8) | 71.5 (4.43; 65-77; 6) | * |

FLIPPER(U), method unknown, TARSUS = greatest length from front (Falla 1937).

Tail-length an unreliable biometric because it changes with wear; some data in Falla (1937).

WEIGHTS In kg, except where stated. Weight of adults at first arrival at breeding grounds greatest in earliest arrivers. Mean weights: 22 Oct.: males 6.0 (n=16); females 5.4 (n=4); 22 Nov.: males 4.0 (n=15); further information on weights available (Ainley & Emison 1972). Loss of weight during incubation: males 44 g/day; females 64 g/day. Weights of adults feeding chicks: 4.49 (3.62-5.44; 51; Penney 1967). Pooled results from 7-11 Jan., non-breeding adults and adults that had just fed chicks: males 4.1 (n=14); females 3.7 (n=24) (Ainley & Emison 1972). Pre-moult: adults 3.67 (2.72-4.31; 57); juveniles 3.08 (2.6-3.52; 12). Loss of weight during moult about 150 g/day; total loss during moult in adults and juveniles about 45%.

STRUCTURE Short erectile crest on nape. Bill, short and heavy; feathering encroaches over half of bill length. Upper mandible decurved at tip. Tail, long (c. 170 mm when full length). Middle toe longest; outer toe c. 87%; inner toe c. 73%. Vestigial hind claw dangles on inner side of foot.

GEOGRAPHICAL VARIATION None. *P. adeliae* and *P. antarctica* said to form a superspecies (Peters).

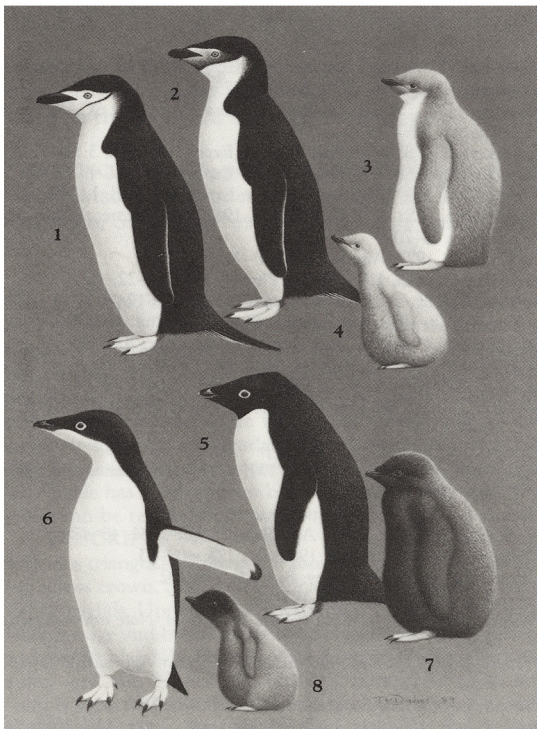
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REFERENCES

- Ainley, D.G. 1974. *Behaviour* 50: 16-51.
 Ainley, D.G. 1975. Pp. 139-57. In: Stonehouse 1975.
 Ainley, D.G., & W.B. Emison. 1972. *Ibis* 114: 267-71.
 Ainley, D.G., & R.E. LeResche. 1973. *Condor* 75: 235-9.
 Ainley, D.G., & R.P. Schlatter. 1972. *Auk* 89: 559-66.
 Ainley, D.G., et al. 1978. *Wilson Bull.* 90: 492-510.
 Ainley, D.G., et al. 1983. *Breeding Biology of the Adelie Penguin*.
 Ainley, D.G., et al. 1984. *AOU orn. Monogr.* 32.
 Andersson, K.A. 1908. *Wiss. Ergeb. Schwed. Sudpolarexped. 1901-1903*, 5, *Zool.* 1: 1-58.
 Artemyev, A. 1964. *Soviet Antarct. Exped. Infor. Bull.* 5: 218-9.
 Bierman, W.J.H., & K.H. Voous. 1950. *Ardec* 37: 1-123.
 Caughley, G. 1980. *Rec. Dominion Mus.* 3: 262-82.
 Clark, B.D., & W. Bemis. 1979. *J. Zool., Lond.* 188: 411-28.
 Clarke, W.E. 1906. *Ibis* (Ser. 8) 6: 145-87.
 Cline, D.R., et al. 1969. *Auk* 86: 701-16.
 Conroy, J.W.H. 1975. Pp 321-36. In: Stonehouse 1975.
 Cooper, J. 1985. *Emu* 85: 205-6.
 Cowan, A.N. 1979. *Aust. Bird Watcher* 8: 69-90.
 Cowan, A.N. 1983. *Corella* 7: 59-61.
 Crawford, R.D. 1974. *Notornis* 21: 381-2.
 Croxall, J.P. 1985. *Biologist* 32: 165-70.
 Croxall, J.P. (Ed.). 1987. *Seabirds: Feeding Ecology and Role in Marine Ecosystems*.
 Croxall, J.P., & E.D. Kirkwood. 1979. *The Distribution and Abundance of Penguins on the Antarctic Peninsula and Islands of the Scotia Sea*. Br. Antarct. Surv.
 Croxall, J.P., & G.S. Lishman. 1987. Pp. 101-33. In: Croxall 1987.
 Croxall, J.P., et al. 1984. *ICBP Tech. Publ.* 2: 637-66.
 Davis, L.S. 1988. *Auk* 105: 428-32.
 Davis, L.S., & F.T. McCaffrey. 1986. *Auk* 103: 379-8.

| | MALES | FEMALES | |
|------------|------------------------------|-------------------------|----|
| FLIPPER(D) | (1) 211 (6.5; 195-221; 28) | 204 (6.8; 192-213; 16) | ** |
| FLIPPER(U) | (2) 188.4 (7.11; 180-200; 8) | 192 (4.47; 183-196; 6) | * |
| BILL | (1) 35.5 (2.8; 31-40; 31) | 32.9 (2.4; 28-37; 18) | ** |
| | (2) 39.5 (2.64; 36-43; 8) | 34.8 (1.87; 32.5-38; 6) | ** |

- Davis, L.S., & J.T. Darby (Eds). In press. *Penguin Biology*.
- Davis, L.S., et al. 1988. *Notornis* 35: 15-23.
- Dombrowski, A.B. 1925. *Wyprawy Polarne*.
- Downes, M.C., et al. 1959. *ANARE Rep., Ser. B*, 1.
- Eklund, C.R. 1945. *Proc. Am. Phil. Soc.* 89: 299-304.
- Emison, W.B. 1968. *Antarct. Res. Ser. Washington* 12: 191-212.
- Emlen, J.T., & R.L. Penney. 1966. Pp 323-31. In: Wessels 1966.
- Falla, R.A. 1937. *Rep. B.A.N.Z. Antarct. Res. Exped., Ser. B*, II.
- Fedak, M.A., et al. 1974. *Antarct. J. US* 9: 97-8.
- Gain, L. 1914. *Oiseaux Antarct. Deux. Exped. Antarct. Fr.* (1908-1910). 2, 1-200.
- Green, K., & G.W. Johnstone. 1988. *Aust. Wildl. Res.* 15: 103-10.
- Green, K. 1986. *Notornis* 33: 90-1.
- Gwynn, A.M. 1953. *ANARE Rep.*, B, 1: 1-29.
- Haftorn, S., et al. 1981. *Norsk Polarinstitut Skrift* 175: 29-35.
- Harper, P.C., et al. 1984. *ICBP Tech. Publ.* 2: 593-608.
- Harrington, H.J. 1960. *Notornis* 9: 33-9.
- Holgersen, H. 1951. *Proc. Int. orn. Congr. X*: 614-16.
- Horne, R. 1980. *Prelim. Surv. Dist. Penguins Aust. Antarct. Terr., Macquarie I., Heard I., MacDonald I.* Unpubl. Rep. BIOMASS Working Party Bird Ecol.
- Horne, R.S.C. 1983. *ANARE Notes* 9: 1-82.
- Jablonski, B. 1984. *Polish Polar Res.* 5: 5-30.
- Jablonski, B. 1985. *Acta Zool. Cracov.* 29: 117-86.
- Jablonski, B. 1987. *Acta Zool. Cracov.* 30: 97-118.
- Jazdzewski, K. 1981. *Polish Polar Res.* 2: 133-44.
- Johnstone, G.W., et al. 1973. *ANARE Scient. Rep., Ser. B*, 1, 123: 1-62.
- Jouventin, P., et al. 1984. *ICBP Tech. Publ.* 2: 609-25.
- Jouventin, P. 1982. *Visual and Vocal Signals in Penguins*.
- Kamenev, V.M. 1971. *Soviet Antarct. Exped. Infor. Bull.* 8: 219-22.
- Kennington, S.R. 1963. *Notornis* 10: 234.
- Korotkevich, E.S. 1964. *Soviet Antarct. Exped. Infor. Bull.* 1: 149-52.
- Korotkevich, E.S. 1980. *Data Penguin Colonies.* Unpubl. Rep. BIOMASS Working Party Bird Ecol.
- Law, P. 1964. *ANARE Rep. Ser. A*, 1: 1-67.
- Learmonth, N.F. 1955. *Emu* 55: 100-4, 277-8.
- LeResche, R.E., & W.J.L. Sladen. 1970. *Anim. Behav.* 18: 517-26.
- Levick, G.M. 1914. *Antarctic Penguins*.
- Levick, G.M. 1915. *Br. Antarct. 'Terra Nova' Exped., 1910, Zool.* 1: 55-84.
- Lindsey, T.R. 1986. *The Seabirds of Australia*.
- Lishman, G.S. 1985a. *Ibis* 127: 84-99.
- Lishman, G.S. 1985b. *J. Zool., Lond.* 205A: 245-63.
- Llano, G.A. (Ed.). 1977. *Adaptations within Antarctic Ecosystems*.
- Matthews, L.H. 1929. *Discovery Rep.* 1: 561-92.
- Mawson, D. 1915. *The Home of the Blizzard*.
- Menegaux, A. 1907. *Oiseaux* 4: 1-79.
- Montague, T.L. 1988. *Hydrobiologia* 165: 227-37.
- Mougin, J-L. 1968. *Oiseaux Revue fr. Orn.* 38: 89-94.
- Muller-Schwarze, C., & D. Muller-Schwarze. 1975. Pp 309-20. In: Stonehouse 1975.
- Murray, J. 1909. *The Heart of the Antarctic*. 2.
- Naito, Y., et al. 1988. *Abstracts Fifth SCAR Symp. Antarct. Biol.*
- Nudelman, A.V. 1962. *Soviet Antarct. Exped. 1959-1961*.
- Obst, B.S. 1985. *Auk* 102: 540-9.
- Oelke, H. 1975. Pp. 363-95. In: Stonehouse 1975.
- Offredo, C., et al. 1985. *Mar. Biol.* 86: 199-202.
- Parmelee, D.F., et al. 1977. *Antarct. J. US* 12: 14-21.
- Parmelee, D.F., & J.M. Parmelee. 1987. *Br. Antarct. Surv. Bull.* 76: 65-73.
- Paulian, C.D. 1975. *Mauri ora* 3: 27-30.
- Penney, R.L. 1967. *Auk* 84: 61-71.
- Penney, R.L. 1968. *Antarct. Res. Ser. Washington* 12: 83-131.
- Peterson, R.T. 1979. *Penguins*.
- Poncet, S., & J. Poncet. 1985. *Br. Antarct. Surv. Bull.* 68: 71-81.
- Poncet, S., & J. Poncet. 1987. *Br. Antarct. Surv. Bull.* 77: 109-29.
- Prince, P.A., & J.P. Croxall. 1983. *Br. Antarct. Surv. Bull.* 59: 15-27.
- Pryor, M.E. 1968. *Antarct. Res. Ser. Washington* 12: 57-82.
- Puddicombe, R., & G.W. Johnstone. 1988. *Hydrobiologia* 165: 239-53.
- Reid, B.E. 1964. *Rec. Dom. Mus.* 5: 11-37.
- Reid, B.E. 1965. *NZ J. Sci.* 8: 503-14.
- Richdale, L.E. 1951. *Sexual Behavior of Penguins*.
- Ridoux, V., & C. Offredo. 1989. *Polar Biol.* 9: 137-45.
- Rootes, D.M. 1988. *Br. Antarct. Surv. Bull.* 80: 87-119.
- Sadlier, R.M.F.S., & K.R. Lay. 1988. *Abstracts Fifth SCAR Symp. Antarct. Biol.*
- Sapin-Jaloustre, J., & F. Bourliere. 1951. *Alauda* 19: 65-83.
- Sapin-Jaloustre, J. 1960. *Ecologie du Manchot Adélie*.
- Sladen, W.J.L. 1953. *Nature* 171: 952-5.
- Sladen, W.J.L. 1958. *Sexual Behavior of Falkland I. Depend. Surv.* 17: 1-97.
- Sladen, W.J.L., et al. 1968. *Antarct. J. US* 3: 6, 247-9.
- Spellerberg, I.F. 1971. *Emu* 71: 167-71.
- Spurr, E.B. 1975. *Ibis* 117: 324-38.
- Stonehouse, B. 1963. *Proc. Int. orn. Congr. XIII*: 766-79.
- Stonehouse, B. 1966. *Nature* 210: 925-6.
- Stonehouse, B. (Ed.) 1975. *The Biology of Penguins*.
- Strandtmann, R.W. 1978. *Antarct. J. US* 13: 151-3.
- Syrojeckovskij, E.E. 1966. Pp. 103-129. In: *Antarktika*.
- Taylor, R.H. 1962a. *Ibis* 104: 176-204.
- Taylor, R.H. 1962b. *Notornis* 10: 111-13.
- Taylor, R.H., & H.S. Roberts. 1962. *NZ J. Sci.* 5: 191-7.
- Taylor, R.H., et al. In press. In: Davis & Darby in press.
- Tenaza, R. 1971. *Condor* 73: 81-92.
- Thomson, R.B. 1977. Pp 1177-80. In: Llano 1977.
- Trivelpiece, W.Z., et al. 1983. *Antarct. J. US* 18: 209-10.
- Trivelpiece, W.Z., et al. 1987. *Ecology* 68: 351-61.
- Tuffy, R., & P. Fazackerly. 1984. *Tas. Bird. Rep.* 13: 24-5.
- Valencia, J., et al. 1988. *Abstracts Fifth SCAR Symp. Antarct. Biol.*
- Valette, L.H. 1906. *Zool. Bacteriol. Vet. Zool.* 3: 40-64.
- van Heezik, Y. 1988. *Notornis* 35: 23-6.
- Volkman, N.J., & W. Trivelpiece. 1980. *J. Zool., Lond.* 191: 521-30.
- Volkman, N.J., & W. Trivelpiece. 1981. *Wilson Bull.* 93: 243-8.
- Volkman, N.J., et al. 1980. *Condor* 82: 373-8.
- Volkman, N.J., et al. 1982. *Antarct. J. US* 17: 180.
- Ward, G.D., et al. 1986. *NZ Antarct. Rec.* 7: 14-18.
- Wessels, N.K. (Ed.) 1966. *Vertebrate Structures and Functions*.
- White, M.G., & J.W.H. Conroy. 1975. *Ibis* 118: 371-3.
- Whitehead, M.D. 1989. *Polar Biol.* 9: 1-4.
- Whitehead, M.D., et al. In press. *Annual fluctuations in productivity and breeding success of Adélie Penguins and Fulmarine Petrels in Prydz Bay, East Antarctica*.
- Whittell, H.M. 1937. *Emu* 37: 65-6.
- Wilson, E.A. 1907. *Br. natn. Antarct. Exped. Rep. 1901-1904, Nat. Hist., Zool.*, 2 (2): 1-121.
- Wilson, G.J. 1983. *BIOMASS Sci. Ser.* 4:
- Wilson, G.J., & R.H. Taylor. 1984. *NZ Antarct. Rec.* 6: 1-7.
- Wilson, G.J., et al. In press a. *Proc. Fifth SCAR Symp. Antarct. Biol.*
- Wilson, R.P., et al. In press b. *Polar Biol.*
- Woehler, E.J. In press. *The Distribution and Abundance of Antarctic and Subantarctic Penguins: An Update*.
- Woods, R.W. 1975. *The Birds of the Falkland Islands*.
- Yeates, G.W. 1975. Pp 397-409. In: Stonehouse 1975.
- Yeates, G.W. 1968. *Mar. Freshwat. Res.* 2: 472-96.
- Zink, R.M. 1981. *Wilson Bull.* 93: 1-20.



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Chinstrap Penguin *Pygoscelis antarctica*

- 1. Adult
- 2. Juvenile
- 3. Downy young, mesoptile
- 4. Downy young, protoptile

Adelie Penguin *Pygoscelis adeliae*

- 5. Adult
- 6. Juvenile
- 7. Downy young, mesoptile
- 8. Downy young, protoptile

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