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.

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Rijke, R.M. 1970. *J. Exp. Biol.* 52: 469–79.
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Aptenodytes forsteri Emperor Penguin

Aptenodytes forsteri G.R. Gray, 1844, *Ann. Mag. nat. Hist.* 13: 315 — no locality; Antarctica seas.

The generic name is a combination of the Greek ἀπτήν (unfledged, callow or unwinged) and δύτης (a diver). The species was named in honour of J.R. Forster who accompanied Captain Cook in HMS Resolution from 1772 to 1775, as a naturalist.

MONOTYPIC.

FIELD IDENTIFICATION   Length 100–130 cm; flipper 30–40 mm; weight: males *c.* 38 kg, females *c.* 30 kg. Largest penguin; very robust with black head and large yellow-white patches on sides of neck. Head appears small in relation to body and feet. Slender, curved bill, black with conspicuous orange, pink or lilac mandibular plate. Black feathers of chin extend onto mandible. Upperparts, blue-grey; underparts white. Tarsus feathered on outside. Sexes similar. Immature similar to adult but duller. No seasonal changes of plumage. Breed only on Antarctic continent and rarely found further N. Larger and less brightly coloured than more northerly King Penguin *A. patagonicus.*
    DESCRIPTION   ADULT. Head, chin and throat black, sharply demarcated from yellow-white upper breast
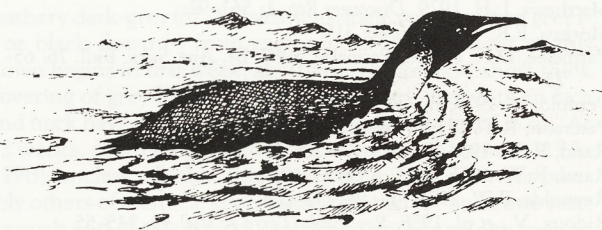
and auricular patch. Broad, yellow auricular patch (4 cm wide), brightest near head, fading to pale yellow along broad stripe that leads to upper breast. Lower margin of auricular patch blends into grey-blue dorsal plumage but black strip separates upperparts from white underparts between neck and flipper.

Black strip extends upwards partly to separate auricular patch from upper breast. Dorsal plumage, from nape to tail, including flippers, dark grey-blue; tail, black. Breast and abdomen satin white, tinged yellow on upper breast. Underflippers white with fine grey line along leading-edge and small dark patch at tip. Bill, slender and decurved; upper mandible black, lower mandible pink, orange or lilac. Chin feathers, black, partially covering lower mandible. Iris, brown. Feet black with outer side of tarsus feathered. Before moult (Dec.–Feb.) dorsal plumage turns brownish. FLEDGELING. Smaller than adult, but plumage similar. Auricular patches, yellowish grey; throat, white to grey; crown, grey; bill, black.
    SIMILAR SPECIES   Can be confused only with smaller, more brightly coloured **King Penguin**; ranges may overlap off s. tip of South America. Emperor Penguin distinguished by shorter, more downcurved bill and only narrow strip of colour, usually pink, exposed on lower mandible compared with broad, orange mandibular plate of King Penguin; auricular patch of Emperor Penguin larger, paler and not clearly separated from dorsal plumage and black throat sharply demarcated from upper breast. From behind, considerable area of white shows on sides of neck, whereas in King Penguin only a little yellow shows. Outside of tarsus feathered in Emperor Penguins, bare in King. Immatures differ in shape of auricular patches and in feathering of tarsus (as in adults). At sea, auricular patches of Emperor Penguins appear large and pale, almost meeting on nape and extending to water line. In comparison, auricular patches of King Penguins, smaller and brighter with darker plumage visible all round. Emperor Penguins breed only on Antarctic continent and rarely reported further N, whereas King Penguins breed in lower latitudes on subantarctic islands.
    Breed at about 40 localities round Antarctica. Tend to remain within open-ice areas of Antarctic Zone. Can stay

underwater for long periods and dive deeply. Walk or toboggan on snow and ice; do not hop. Voice, various crowing, trumpeting and short calls on land.

HABITAT Marine; circumpolar in pack-ice of Antarctic Zone. N. limit of distribution the limits of pack-ice. Highest densities near breeding colonies. Most birds found within pack-ice. No apparent preference for particular concentration of ice (Ainley *et al.* 1984). In Weddell Sea: mostly in medium pack-ice (40–60%), with ample open water for feeding; also in light (10–30%) and heavy (70–100%) pack-ice (Cline *et al.* 1969). In Ross and Amundsen Seas, most in light pack (12–50%), fewer in heavy pack (60–100%) (Zink 1981). Generally avoid open water outside limits of floating ice; keep to perimeters of open water within pack-ice (Cline *et al.* 1969); rare in open waters of continental slope a few kilometres from ice (Ainley *et al.* 1984). Off Terre Adélie, not observed foraging in inshore waters, even when sea-ice breaking up; thought to feed at greater distances offshore; not seen using tide cracks beside icebergs for feeding (Offredo & Ridoux 1986). When breeding, thought to prefer feeding in sea beyond fast-ice, but, if distant or inaccessible, use seal holes, pools in sea-ice, open leads and tide cracks (Budd 1961; Jouventin 1975; Cracknell 1986). Can dive under large floes and between isolated holes in large ice sheets (Kooyman *et al.* 1971).

Breed Antarctic continent, Peninsular coast and continental islands, during s. winter in extremes of cold (to -62 °C; Murphy), wind (to 180 km/h; Jouventin 1975) and darkness. Colonies need: accessible fairly level surface; safety from premature break-up of sea-ice during breeding; shelter from wind, particularly for chicks; accessible open water for feeding. Sea-ice usually chosen, as most coasts too rocky and steep, and shelf-ice and slopes and plateaux of mainland inaccessible; but at Taylor Glacier, in dry valley and at Dion Is on snow-covered shingle (Budd 1961). Stable sea-ice preferred; most colonies near elevated features (islands, icebergs, cliffs, steep hills, headlands) or on sea-ice partly enclosed by shelf-ice, reefs or curves of bays (Caughley 1960; Stonehouse 1969), which increases stability. At Franklin I., large colony where break-up of ice probably often occurs before chicks complete moult (Stonehouse 1969). Adults may not need shelter from wind, but chicks vulnerable. Islands, cliffs and icebergs near colonies reduce wind-speed; shelter from wind probably a factor in choice of site; colonies under cliffs in danger from rock slides and avalanches (Todd 1980). At Taylor Glacier, birds stand on sunny slopes; but many colonies shaded, and exposure to sun may not be important. Probably best fishing grounds are beyond fast-ice; but sites at ice-edge may be subject to early break-up; so choice of sites is a compromise. In colonies far from open water (up to 200 km at Pte Géologie; Jouventin 1975), seal holes, tide cracks, leads and pools used, although food may be less plentiful than in open sea. At Amanda Bay, open sea accessible (38 km), but birds feed at seal holes en route (Cracknell 1986).

Adults moult on fast or floating ice, or on continental shores. Diving depths at C. Crozier, 45–265 m; greatest depth recorded for any aquatic bird species. More recent work has recorded diving depths of >400 m (G. Robertson). May forage in shallow water, 20 m depth, searching bottom for food (Kooyman *et al.* 1971).

DISTRIBUTION AND POPULATION Cirucmpo-

lar; in Antarctic zone within limits of pack-ice. Breed round shores of Antarctic Continent, Peninsula and adjacent islands between 66°S and 78°S. Recorded at islands of maritime Antarctic and Subantarctic. Accidental to NZ, South America; no confirmed records Aust.

Circumpolar in cold waters of Antarctic Zone, S of Antarctic Convergence; rarely outside limits of pack-ice. S. limits of range, barrier of Antarctic Ice Shelf in 78°S; n., limits of pack-ice. In Ross Sea, birds seen only S of 70°S; distribution coincided with continental slope and overlying pack-ice. Generally observed between Antarctic coasts and latitude 65°S; considerably less often between 65° and 60°S and exceptional farther N. Recorded S. Orkney Is (Clarke 1906, 1907); S. Sandwich Is (Cordier *et al.* 1981); Heard I. (Downes *et al.* 1959); S. Georgia, 8 records (Rankin 1951; Prince & Payne 1979; Prince & Croxall 1983; Clark 1986); Iles Kerguelen (Hall 1909; Falla 1937; Derenne *et al.* 1974); Falkland Is (Hamilton 1954; Cawkell & Hamilton 1961). Accidental to Tierra del Fuego (Reynolds 1935; Venegas 1978). Most northerly observation, three immatures off Argentina (40°30'S, 54°34'W), may have been ship-assisted (Rumboll & Jehl 1977).

NZ Oreti Beach, Southland, SI, 5 Apr. 1967 (Henderson 1968).

BREEDING Localities summarized in Table 1: 42 colonies reported; breeding doubtful at 5; 35 colonies extant: 21 between 65°S and 70°S; 8 between 70° and 75°S; 6 S of 75°S. No colonies known between 180° and 90°W.

No longer breeding at Inaccessible I. (four pairs 1973, one egg laid 1974) (Jonkel & Llano 1975). Colonies reported, but breeding not confirmed at Ongul I. (= Showa Base) (Haga 1961); Marble Point (= McMurdo Sound) (Harrington 1959); Edward VII Peninsula (Wilson 1907; Korotkevich 1962; Watson *et al.* 1971); Norsel Bay (Giaever 1954); and Lasarev Sea (Konavalov 1964).

POPULATION Total population estimated 135 000 (Wilson 1983) to 175 000 breeding pairs (J-L. Mougin) and *c.* 400 000–450 000 breeding and non-breeding individuals (J-L. Mougin). Ross Sea sector contains six colonies with about 80 000 pairs or half total number of breeding pairs (Harper *et al.* 1984).

Status, stable; some colonies appear to fluctuate in numbers but this may be result of inaccurate counts. Protected by winter breeding in remote localities. Colonies probably susceptible to human disturbance, especially near bases. In Ross Sea Sector, populations almost halved since 1975, possibly for this reason (Jouventin *et al.* 1984).

MOVEMENTS Considered dispersive but little information on non-breeding movements. Breeding grounds deserted for only three months at a time so probably do not travel far.

DEPARTURE Non-breeders or unsuccessful breeders leave colonies Oct.–early Nov. drifting N on ice-floes; breeding birds and young remain at colonies until early Dec. (Murphy), late Dec. (Pte Géologie; Prévost 1953) or early Jan. (C. Crozier, Ainley *et al.* 1978; Dion Is, Stonehouse 1953; Haswell I., Korotkevich 1958, Pryor 1968). Fast during moult, mid-Nov. to mid-Jan. (Falla 1937), return to fast sea-ice (Cracknell 1986) but not necessarily to colony (Falla 1937). May again float N if ice breaks up, otherwise apparently remain near continent until breeding season (Murphy).

NON-BREEDING In Ross Sea, concentrate during
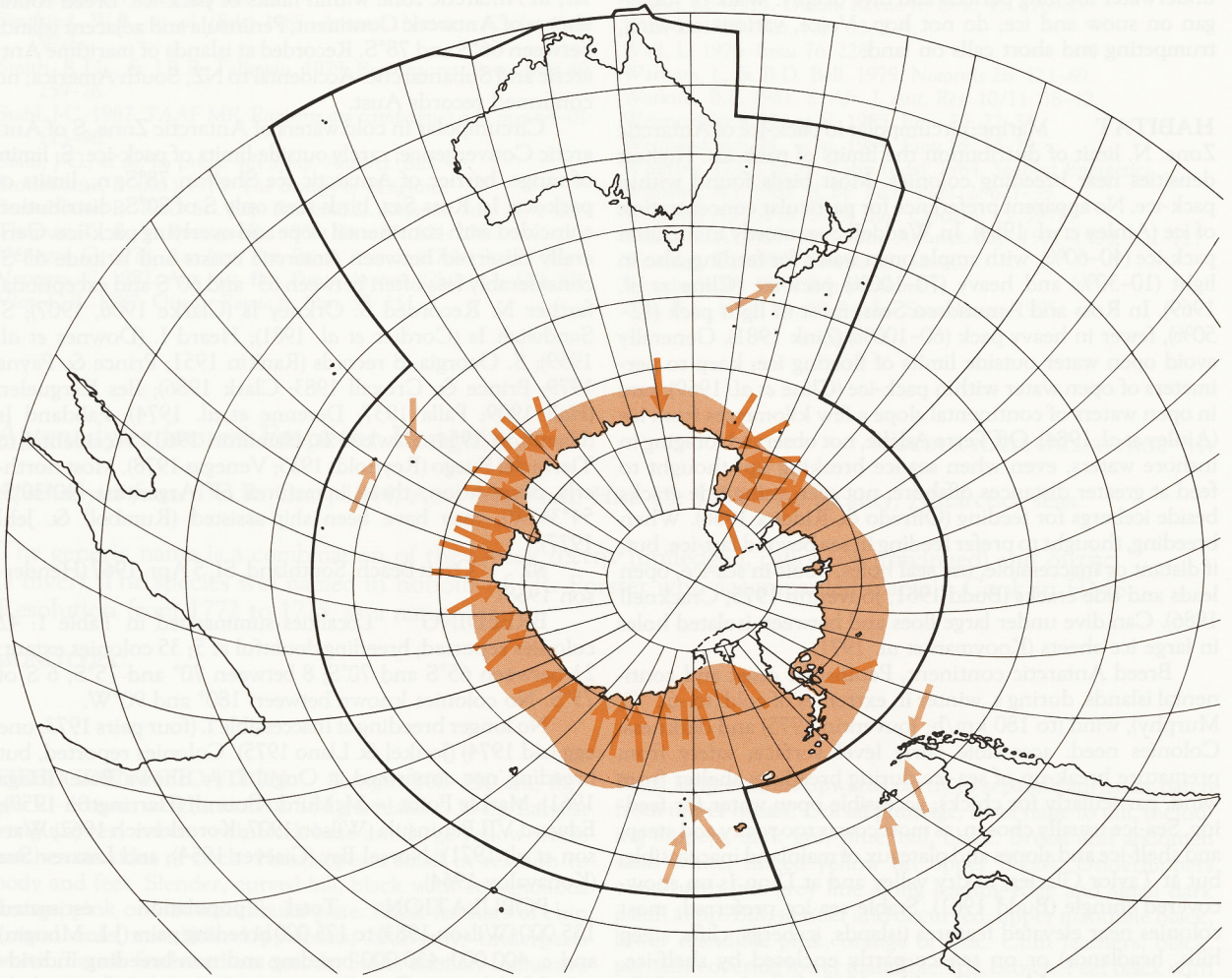
summer at shelf-slope and Antarctic Divergence (Ainley &
Jacobs 1981), most adults less than 300 km from breeding site;
beyond 300 km, one third of birds were immatures (Ainley et
al. 1984). Seven of 15 records outside usual range in Apr.; six
in Jan.–Mar.; two in July (Hall 1909; Reynolds 1935; Hamilton
1954; Downes et al. 1959; Henderson 1968; Prince & Payne
1979; Prince & Croxall 1983; Clark 1986).

RETURN   Arrive Haswell I., late Mar. (Korotkevich
1958; Pryor 1968); Mirny, 20 Mar. (Nudelman 1962); Terre
Adélie, early Apr. (Prévost 1953) but leaving early May before
returning to lay late May (Dion I.; Stonehouse 1960), early
June (Terre Adélie; Prévost 1961) or late June (C. Crozier;
Ainley et al. 1978). Travel up to 200 km across ice to reach
breeding areas (Prévost 1961), possibly assisted by swimming
between open leads (Willing 1958). In winter, possibly regular
visitor to S. Shetland and S. Orkney Is, at least half those at
Signy I., S. Orkney Is, being immature (Rootes 1988). Im-
matures noted at sea as far N as 40°S in spring (Rumboll & Jehl
1977).

BREEDING   Foraging range estimated at 50 km
(Gales et al. 1990) to 300 km (Ainley et al. 1984), probably to
continental shelf and shelf-break (Ainley & Jacobs 1981).

FOOD   Varies with locality, at some sites mostly notothe-
niid fish, at others mostly euphausiid crustaceans; at all sites
also small cephalopods. BEHAVIOUR. Feed by pursuit-diving,
appearing to have two principal strategies: searching beneath
ice-floes for euphausiids and small pelagic fish and deep diving
for cephalopods and meso-pelagic fish (Klages & Gales 1988;
Klages 1989). Dive up to 265 m (capillary recorder) usually for
2.5–9.0 min but up to at least 18 (Kooyman et al. 1971) at
speeds up to 2.26 m/s in captivity (Clark & Bemis 1979), 2.67
m/s during experiments in wild, rising to surface at up to 2
m/s (Kooyman et al. 1971). Even when open water available
inshore, appear to feed away from coast (Offredo & Ridoux
1986), preferring pack-ice (Ainley et al. 1984), though seen
using tidal cracks near coastal icebergs (Willing 1958) and seal
holes while travelling to and from breeding areas (Willing
1958; Cracknell 1986). Sometimes appear disoriented under
ice (Kooyman et al. 1971), possibly explaining preference for
feeding in open water. Often observed feeding in groups, with
diving apparently co-ordinated (Kooyman et al. 1971).

NON-BREEDING   Known only from incidental ob-
servations: fish and cephalopods in adults collected in conti-
nental waters; small fish and euphausiids in birds taken among
pack-ice (Murphy); 15 cm fish without heads (one adult,
McMurdo Sound; Falla 1937); 17 cm cephalopods (Bierman
& Voous 1950); cephalopod beaks (Friedman 1945).

BREEDING   Summarized Table 2. At **Terre Adélie**
late in breeding season (29 stomachs; Offredo & Ridoux

Table 1.

Locality	Year of Estimate	Estimate (pairs)	Reference
Dronning Maud Land			
Riiser-Larsen (not Riiser-Larsen Pen.)		11 800	15
Atka Bay		16 000	15
SANAE		113	6
Lasarev Ice Shelf		4000–5000	23 25,28
Riiser-Larsen Pen.		5750	17
Enderby Land			
Casey Bay	No recent reports		3,27,53,55
Amundsen Bay	No recent reports		3,53,55
Kemp Land:			
Kloa Pt	1957	5000 birds	51
		2500	2
		3050	3,53
	1985	4500	56
Fold I.	1957	2000 birds	51
	1959–60	1000	2,3,53
	1977	450	16
	1985	348	56
Taylor Glacier	1954	c. 5000 birds	4,51
		4000	2
	1960	4000 adults	3,53
	1980	1725	16
	1988	3000	39
Auster Rookery (Douglas Is)	1957	20 000 birds	51
	1957–60	10 000–12 000	2,3,25,53
	1965	30 000 adults	4
	1978	10 000–12 000	16
	1988	12 000	39
MacRobertson Land:			
Cape Darnley	1958	c. 5000	2,51
Sandefjord Ice Bay		200	53
Vestfold Hills		1000–2000 birds	51
Amanda Bay	1958	c. 1000–2000 birds	51
	1960	c. 3000	2
	1983	2339	8
	1987	9000	56
Princess Elizabeth Land:			
Pingvin I.		15 000	25
Karelin Bay		500	25
Willhelm II Land:			
Gaussberg		2000	25
Queen Mary Land:			
Haswell I.		c. 7000	2,3
		9000	56
	1970	17 000	50
Shackleton Ice Shelf		5000	25,32
Wilkes Land:			
Bowman I.		1500	25
Terre Adélie:			
Pointe Géologie Arch.	1952–75	c. 6000	18,19,21,33,36
	1980s	2500	18,19,21,33,36
	1983	2300	20
	1984	3119	47
George V Land			
Ninnis Glacier			55
Oates Land			
Wilson Hills		90	57
Yule Bay			54
Victoria Land:			
C. Roget		17 000	38
	1964	11 700	9
	1983	3777	24
Coulman I.	1983	21 708	24
C. Washington		4000–6000	9
	1968	2500–3800	41

	1983	19 364	24
Franklin I.		2000+	46
	1983	4893	24
Beaufort I.	1976	1200–1500	45,49
	1983	175	24
C. Crozier	1902, 1903	400, 1000 adults	52
	1957–58	c. 500	5
	1961–63	1450–1500	44
	1974	256	1,29,40,49
	1977	40	49
	1983	78	24
Graham Land:			
Dion I.		500	7
		150	10,42,43
Coats Land:			
Gould Bay (= Bahia Austral)		7500	13,30
Dawson–Lambton		23 400	15
Halley Bay (= Emperor Bay)		10 000	2
		15 000–20 000	7,12,31,34,48,53
	1977	23 500	11
	1986–87	14 300–31 400	15
Stancomb–Wills Prom.		3000	15
Drescher Inlet		13 200	14,15,22

References: (1) Ainley *et al.* (1978); (2) Budd (1961); (3) Budd (1962); (4) Cameron (1969); (5) Caughley (1960); (6) Condy (1979); (7) Conroy (1975); (8) Cracknell (1986); (9) Cranfield (1966); (10) Croxall & Kirkwood (1979); (11) Croxall *et al.* (1984); (12) Dalgleish (1956); (13) Eklund (1959); (14) Gerdes *et al.* (1987); (15) Hempel & Stonehouse (1987); (16) Horne (1980); (17) Hoshiai & Chujo (1976); (18) Jouanin & Prévost (1953); (19) Jouventin (1971); (20) Jouventin & Weimerskirch (in press); (21) Jouventin *et al.* (1984); (22) Klages & Gerdes (1988); (23) Konovalov (1964); (24) Kooyman & Mullins (in press); (25) Korotkevich (1962); (26) Korotkevich (1964); (27) Koretkevich & Ledenev (1962); (28) Ledenev (1960); (29) Le Resche *et al.* (1970); (30) Luna Perez (1963); (31) Marples & Falla (1944); (32) Mawson (1942); (33) Mougin (1966); (34) Novatti (1959); (35) Nudelman (1962); (36) Prévost (1959); (37) Pryor (1968); (38) Quartermain (1964); (39) G.R. Robertson; (40) Sladen *et al.* (1968); (41) Stirling & Greenwood (1970); (42) Stonehouse (1953); (43) Stonehouse (1960); (44) Stonehouse (1964); (45) Stonehouse (1966); (46) Stonehouse (1969); (47) Thomas (1986); (48) Tickell (1960); (49) Todd (1980); (50) Unpubl. ANARE data; (51) Willing (1958); (52) Wilson (1907); (53) Wilson (1983); (54) Wilson & Taylor (1984); (55) Woehler (in press); (56) Woehler & Johnstone (in press); (57) Woehler *et al.* (in press).

1986): fish, Stomiatidae 1% no., 45% freq., 10.0–12.0 cm, Nototheniidae 64, 100, 4.0–12.5 cm (incl. *Pagothenia borchgrevinki*), Bathydraconidae <1, 21, 9.0–10.0 cm (incl. *Gymnodraco acuticeps*), Channichthyidae 1, 52, 15.0–20.0 cm; crustaceans, amphipods Hyperiidea <1, <1, 38 (incl. *Hyperia macrocephala*), Gammaridea <1% wt., 3% no., 82% wt. (incl. *Eusirus perdentatus, E. tridentatus, Waldeckia obesa, Uristes gigas, Epimeriella macronyx*), euphausiids 2, 31, 76, mostly *Euphausia superba* 3.96 cm (0.29; 15), some *E. crystallorophias*; cephalopods, *Kondakovia longimana* 0.6, <0.1, 3, *Gonatus antarcticus* 0.8, <0.1, 10, *Psychroteuthis glacialis* 1.5, 0.7, 76, *Histioteuthis* 10.1, <0.1, 7 (Offredo *et al.* 1985). In chicks collected at same site (12, 192 cephalopod beaks; Offredo *et al.* 1985) *Kondakovia longimana* 13.6% wt. of cephalopods, 1.6% no., 25% freq., *Gonatus antarcticus* 17.7, 8.3, 42, *Psychroteuthis glacialis* 68.0, 88.5, 100, *Galiteuthis glacialis* 0.1, 0.5, 8. Many euphausiids probably originally taken by fish but 24% samples contained large numbers suggesting capture by penguin (Offredo & Ridoux 1986).

At **Amanda Bay**, Aug.–Oct. (44 stomach-flushed regurgitations; Gales *et al.* 1989): fish, *Pleuragramma antarcticum* 78.1% wt., 78% no., 75% freq., 7.4 g (2.6, 1.9–19.5, 194), 10.10 cm (1.03, 6.96–13.49), *Trematomus/Pagothenia* 9.5, 2, 25, 23.5–66.1 g, 10.14–15.58 cm, Bathydraconidae 1.1, 1, 1, 1.7–10.8 g, 6.19–11.60 cm, Channichthyidae 7.9, 1, 18, 25.8–68.3 g, 10.14–15.58 cm; cephalopods, *Gonatus antarcticus* <0.1, <1, 2, *Psychroteuthis glacialis* 2.1, 4, 36, 3.75 g (6.17; 1.2–42.3; 58), 4.53 cm (2.15; 2.77–1.74; 58); crustaceans, amphipods Hyperiidea <0.1, <1, 6, Gammaridea 0.3, 10, 41, euphausiids 0.1, 3, 6; crustaceans and two sea urchins Echinoidea probably eaten first by fish. Of fish *P. antarcticum* increased in importance Aug.–Oct., *Trematomus/Pagothenia* declined; cephalopods most important Sept.

At ice edge nearby, Aug.–Oct. (151 faeces; Green 1986) fish, mostly *Pleuragramma antarcticum* 12.95 cm (2.38; 7.23–18.26; 21), some *Pagothenia borchgrevinki* 5.0–10.0 cm, *Trematomus newnesi* 7.0 cm, fish eggs 39.7, crustaceans, incl. mysidaceans 0.7, amphipods 29.8% freq. (Hyperiidae 7.3, Gammaridae 12.6), isopods 21.9, euphausiids 1.3, unident. crustaceans 53.0, cephalopods 3.3 and gastropods 6.7. Gammaridae increased in freq. Aug.–Oct. Faeces possibly from non-breeding birds; faeces from birds feeding chicks contained no identifiable remains suggesting differences in rate of digestion between breeders and non-breeders (Gales *et al.* 1990).

At **Drescher Inlet**, e. Weddell Sea (30 regurgitated samples, 61203 items, Klages 1989) fish, *Notolepis coatsi* 0.2% no., 37% freq., 14.0 g, 20.19 cm, *Pagetopsis maculatus* <0.1, 10, 250.0 g, 16.24–34.49 cm (6), *Pleuragramma antarcticum* 0.5, 53, 24.6 g (0.6–99.6; 556), 14.69 cm (4.87–22.45; 556), *Trematomus* <0.1, 13, 6.1 g (2.7–12.0; 9), 9.17 cm (7.42–11.76; 9), *Chionodraco* <0.1, 7, 1058.7–1240.9 g, 454.7–476.5 cm (3), unident. fish <0.1, 3; cephalopods, *Psychroteuthis glacialis* 1.1, 67, 6.6 g (2.8–12.5; 490), 6.62 cm (4.25–9.26), *Alluroteuthis antarctica* 0.1, 57, 40.0 g (63), *Galiteuthis glacialis* <0.1, 7, 73.6–107.1 g (2); crustaceans, amphipods *Hyperiella* <0.1, 20, *Themisto gaudichaudii* <0.1, 3, *Cyllopus* <0.1, 13, euphausiids *Euphausia superba* 98.1, 90, 0.39 g, 3.85 cm (0.52, 84). Samples formed three distinct groups according to type of prey: in 43% crustaceans dominant, in 33% fish and cephalo-

pods dominant, rest mixed; *N. coatsi* increased in importance Oct. to Nov. while *P. antarcticm* declined.

Other records: 1.2 kg flesh, mainly fish (length 5–15 cm), some cephalopods (incl. *P. glacialis*) and euphausiids (1 ad., Terre Adélie; Sapin-Jaloustre 1952); small sardine-like fish and euphausiids (Haswell I. Pryor 1968); cephalopod beaks (C. Crozier; Kooyman *et al.* 1971); mostly fish (Dion I.; Stonehouse 1953). Immediately after hatching chick given oesophageal secretion by male (if female has not returned from foraging) consisting of protein 59.3% dry wt., lipids 28.3, sugars 7.8, ash 4.8 (Prévost & Vilter 1963).

INTAKE   At Terre Adélie, chicks fed every 2.0 days (1.0; 1–4; 41) in Oct., 1.8 days (0.8; 1–3; 27) in Nov. (Offredo & Ridoux 1986), frequency increasing as open sea gets closer to breeding colonies; at Drescher Inlet, mean feeding interval 1.4 days (Klages 1989). During 147 days of growth, chick fed on 14 occasions (Isenmann 1971). Mean total weight stomach contents 1–2 kg early in season (Prévost 1961) rising to 2350 g (1130; 13) Oct. and 3650 g (696; 12) Nov. (Offredo & Ridoux 1986) with mean daily weight gain 113 g (Stonehouse 1953). Stomach contents at Amanda Bay (after filtration and storage) 1334 g (1146; 12–3236; 44) increasing from 690 g in Aug., to 1013 g Sept., 1762 g Oct. (Gales *et al.* 1990); at Drescher Inlet, 1335 g (1031; 169–3590; 30; Klages 1989).

Table 2. Spring diet of Emperor Penguin

	% wt.			% no.			% freq.			
	1	2	3	1	2	3	1	2	3	4
FISH	95	96.8	38.1	65	83	16.8	100	86	73	96
CEPHALOPODS	3	2.7	9.8	1	4	3.3	93	36	80	53+
CRUSTACEANS	2	0.3	52.1	31	10	80.3	76	41	93	3

(1) Adélie Land (Offredo & Ridoux 1986); (2) Amanda Bay (Gales *et al.* 1990); (3) Weddell Sea (Klages 1989); (4) Amanda Bay (Green 1986).

SOCIAL ORGANIZATION   Well known; studies by Wilson (1907), Stonehouse (1953), Prévost (1961), Jouventin (1971, 1982) and Guillotin & Jouventin (1979). However, most work from one colony, Pte Géologie, Terre Adélie, and geographical variation in behaviour may occur. Gregarious throughout year; during breeding and non-breeding periods; at colonies and at sea. Often forage in groups.

BONDS   Seasonally monogamous. Pair-bonds maintained from formation in Mar. until feeding of chick stops in Dec. At Pointe Gèologie, only 14.5% remate with same partner in successive breeding seasons, probably because territories are unstable and sex ratio out of balance, causing pairs to form quickly. At Pointe Gèologie, females 60.5% of population, males 39.5% (Isenmann 1971). Sex ratio probably also explains occurrence of polygynous groups (one male, two females); these groups short-lived, one female usually ejecting other after few hours (Prévost 1961; Isenmann 1971). Divorce rare, occurring only few days after pairing (Isenmann 1971). First pairing at 5.2 years (1.0, 3–9, 124) (Mougin & van Beveren 1979). Only males incubate; both parents tend young until fledging.

BREEDING DISPERSION   Colonial. No nest; egg incubated on feet of parents, mostly by male. Territorial behaviour varies; territory not fixed to site, but area round bird defended; during pair-formation, laying, change-over at brooding and feeding of chicks, space within pecking distance defended; at other times, territory reduced to area of incubation pouch (Jouventin 1971) when in tight-packed huddles for social thermoregulation. These huddles formed in cold periods during breeding cycle, especially during incubation, (Prévost 1961; Mougin 1966); densities in huddles *c*. 8.7 birds/m² (Stonehouse 1953). At Amanda Bay, about 2300 chicks and 2450 adults occupied area 100 x 150 m (Cracknell 1986). During breeding period, wind, low temperatures, thickness of sea-ice, presence of snow, security, etc., may cause colonies to move; generally follow same routes each year (Prévost 1963; Birr 1968; Jouventin 1971).

ROOSTING   During breeding, roost communally or separately, mainly nocturnally. When incubating, birds stationary. In cold weather, social huddles formed; roost separately at other times. Outside breeding season, roosting behaviour little known; birds solitary or loosely grouped.

SOCIAL BEHAVIOUR   Well known; studies begun 1900s (Wilson 1907), continued by Stonehouse (1953), Prévost (1961) Jouventin (1971, 1982) and Guillotin & Jouventin (1979). Displays conspicuous and easy to observe. Social structure informal, without dominance hierarchy and with simple vocabulary.

AGONISTIC BEHAVIOUR   Low level of aggression except during pair-formation and when feeding young. THREAT DISPLAYS. Bill-shaking, Ear-rubbing, Wing-flapping, Horizontal-head-circling Motion and Attack Posture. **Bill-shaking**: head shaken vigorously in horizontal plane; non-ritualized, displacement activity showing conflict. **Ear-rubbing**: bird rubs ear against shoulder; displacement preening, often appearing in circumstances of conflict and signalling low-level aggression. **Wing-flapping**: alarm signal; birds flap flippers when alarmed or uneasy; movement infectious. **Horizontal Head-circling Motion**: highly ritualized behaviour in which head thrown back, then moved forward in lateral, half-circling motions while uttering grunts; never finishes with blow of bill; may be directed towards individuals, but often performed by solitary birds; signals low-level aggression. Common during pair-formation, copulation, laying, and at change-over. **Attack Posture**: non-ritualized intention movement where bird faces intruder or predator; wings raised ready to strike, neck and bill stretched out to peck or pinch-threat. APPEASEMENT DISPLAY.: bird stands or moves rapidly between conspecifics with flippers slightly spread, head drawn back and bill raised; adopted by birds trying to sneak past brooding birds without being attacked; the single defence posture; little or not ritualized (Jouventin 1982).

SEXUAL BEHAVIOUR   Courtship consists of Ecstatic Display, Face-to-face Display, Waddling-gait Display, Bowing, Mutual Display and Keeping Company. **Ecstatic Display**: un-paired male stops moving through colony, lets head fall onto chest, inhales deeply and utters call with head lowered; may be repeated several times with intervals of several seconds between; used in pair-formation; if receptive female nearby, both may engage in **Face-to-face Display**: male and female face each other and slowly lift heads while progressively contracting neck muscles; stretch as tall as possible, freeze for several minutes, then relax; pair then separates or stays together until egg-laying; when staying together, female follows partner, both adopting Waddling-gait, followed by **Bowing**: one bird bends down, posture immediately imitated by mate; may be repeated often, eventually leading to copulation. Bowing also occurs during laying. COPULATION. Dur-

ing a bow by female, male touches back of her neck with bill; female slides to ground and male mounts, steadying himself occasionally by pinching mate's neck with bill and pressing wings against sides of body; once egg laid, both birds engage in **Mutual Display**, in which duetting occurs; occurs after egg laid; at change-over during incubation, when mates meet after having been apart for several weeks or months, same process repeated, but omitting Face-to-face Display and Waddling gait. During brooding, birds of opposite sexes but of different pairs with young chicks **Keep Company** in absence of mates by performing Mutual Displays like birds really paired. No courtship feeding. No mutual preening.

RELATIONS WITHIN FAMILY GROUPS   Incubation by male. Chick brooded and fed by both parents alternately. Chick recognized by parents. Chicks beg by swinging head vertically and calling; recognize call of own parents but, if starving, will beg from other adults. Fed by regurgitation at time of parents' visits. Chicks trying to become adopted usually driven away by adults. Chicks fledge alone; independent after fledging. No dependence on adults after fledging. Chicks avoid predators by seeking refuge on feet of parents; pecks directed to other chicks during bouts of Keeping Company. Unemployed birds may try to take deserted egg, or brood and feed chicks, but survival of these eggs and chicks rare. After emancipation, chicks try to join crèche. At this stage, can strike other with flippers and pinch with bill, which is quite useless againt giant-petrels *Macronectes* spp except when fully grown.

VOICE   Account based on Jouventin (1982); discussed in detail in Prévost (1961), Jouventin (1971, 1972) and Jouventin *et al.* (1979, 1980). Information supplied by J-L. Mougin. Both sexes have loud trumpeting Contact and Agonistic Calls and loud Display (Courtship) Song. Most calling at breeding sites, though trumpeting Contact Call also given at sea, especially when bathing (bathing call). Contact Call can be heard up to 1 km away. Display Song vital in individual recognition and maintenance of pair-bonds. Function and use of Display Song varies throughout breeding cycle: on arrival (Apr.), used much during period up to pair-formation (Apr.–May) as advertising call, indicating sex and availability of individual. After pair-formation, birds mostly silent till laying (Pre-laying Silence); birds that continue to sing in this period attract un-paired birds, resulting in formation of trios and often disrupting pair; pre-laying silence serves to avoid disruption of pair-bond in absence of territory. After laying (mean c. 20 May), singing begins again with much duetting (Mutual Display or Antiphonal Duet) by pairs so that each partner becomes familiar with mate's song; song now functions mainly in individual recognition. During incubation, after departure of females, (mid-May to early July) males do not sing. Singing increases markedly when female returns (at hatching). Singing decreases slightly with departure of males but at high levels for rest of period with much use in pair and parent-chick recognition. Birds closer than 7 m do not sing at same time to avoid overlap of song and loss of signal (Jouventin *et al.* 1979). Distinct SEXUAL DIFFERENCES. in songs, perceptible to human ears (Prévost 1961); males have fewer syllables per song and structure of songs also differs (details below) (Jouventin *et al.* 1979). INDIVIDUAL DIFFERENCES, in Display Song used for individual identification and parent-chick recognition; songs of individuals nearly invariant (even from year to year); songs of different individuals differ. No geographical variation perceived between songs from Caird Coast and Terre Adélie but
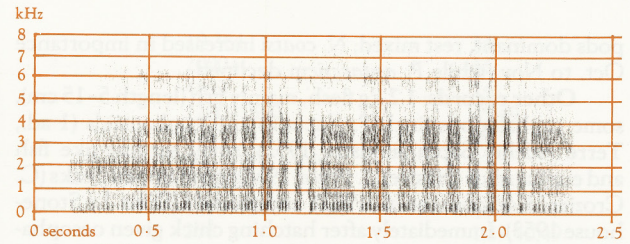
A   G. Robertson; Auster, E. Antarctica, May 1988; X193
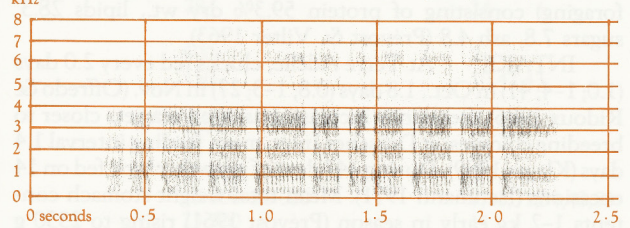
B   G. Robertson; Auster, E. Antarctica, May 1988; X193
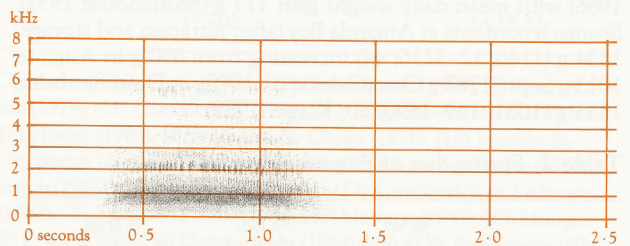
C   G. Robertson; Auster, E. Antarctica, May 1988; X193

sample small (Jouventin 1982).

ADULT   **Display Song.** Powerful and rhythmic buzzing chatter *a-a-a-a...* Duration of songs similar for males and females: 2.09 s (1.35–2.65; 21) 1.82 s (1.26–2.32; 34) respectively. However, distinct sexual differences in number of syllables per song: in females, 20.5 (11–25; 34), in males, 10.7 (7–12; 21); differences also occur in general structure of songs: songs of females mostly consist of two repeats of pattern of one long syllable followed by several short syllables and another long syllable (see sonagram A); occasionally, pattern not repeated; syllables of male longer than those of females, and length of syllables varies within songs usually following a pattern (see sonagram B). Duration of songs and number and length of syllables given by individual virtually do not change, however, frequency of songs does (Jouventin 1982); thus, individual recognition based on structure of song (sequence of syllables) and not frequency (Jouventin *et al.* 1979; Jouventin 1982). Given during Ecstatic and Mutual Displays. **Contact Call.** Loud trumpeting (sonagram C), with bill raised (Wilson 1907); frequency range 500–6000 Hz, with highest intensity c. 2000 Hz; duration of call c. 1 s; not interrupted by pauses. General form, not frequency, stimulates response (Jouventin 1971, 1982). Alarm Call and bathing Call appear to be variations of Contact Call. Used often throughout breeding period and possibly at other times; functions in contacting other birds, permits grouping of birds (Jouventin 1982) and also used to re-unite mates if associated with Display Song (Jouventin *et al.* 1979). Bathing Call given by birds playing and bathing in sea. **Agonistic Call.** Like a distorted abbreviated Display Song but with frequency bands similar to Contact Call; Agonistic Call varies. Mostly uttered with Horizontal Head-circling motion during breeding period.

YOUNG   Modulated whistle varying in amplitude

and frequency (main frequency: 1861 Hz; 1017–3011 Hz). Calls of individuals do not vary but much variation between chicks. Structure of call is established soon after hatching and parents recognize call of their own chick from when chick is a few days old. Call does not change from hatching to departure (Jouventin *et al.* 1979). Whistle functions in individual recognition and in begging for food. Agonistic Calls and trumpeting have been reported in chicks (Prévost 1961); somewhat modified at end of rearing period just before departure. Acquisition of adult calls occurs much later (Prévost 1961).

BREEDING   Well known, chiefly from studies by Stonehouse (1953) and Prévost (1961), with much information by various workers since 1951 from studies at Pte Géologie, which have been annual since 1961. Information supplied by J-L. Mougin. Breeds colonially during winter, usually on sea-ice, not associated with any other species.

SEASON   Birds attend colonies from Mar. to Dec. Laying highly synchronized at each colony, all occurring within one month and at same time each year. However, cycle begins one month later in southernmost colonies than in northernmost (Boyd *et al.* 1970). Arrival at northernmost colonies from beginning of Mar. to end Apr., males apparently a few days before females. No pre-laying exodus. Females stay at colonies from return to just after laying (c. 40 days); males, from return to end of incubation (c. 115 days). Both sexes and all age-classes leave together during Dec., departure sometimes accelerated by early break up of sea-ice.

	A	L	H		Cr		D		A	L	H			Cr		D	
J F M A M J J A S O N D								J F M A M J J A S O N D									
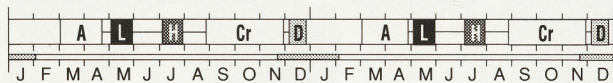
(northern colonies)

SITE   For general statement of sites of colonies see Habitat. Most colonies placed round bases of glaciers, icebergs, cliffs and islands, where tide cracks and leads form readily. At C. Crozier, colony moves in from ice-edge to safer ice as season progresses (Caughley 1960).

NEST, MATERIALS   Nil. Egg held and incubated on adults' feet.

EGGS   Pyriform; smooth texture but often with irregularly spaced tubercles or nodules, mostly at larger end and often in helical line round egg (Prévost 1961); greenish white.

MEASUREMENTS.: at Pte Géologie 122.5 (117.2–132.4; 417) x 82.2 (74.3–89.4).

WEIGHTS.: 442 (300–565; 305) (Mougin 1966).

Albumen, c. 59% of total weight; yolk, 25%; shell, 13%; membranes, 3% (Prévost 1961).

CLUTCH-SIZE   One. No replacement laying, females having left colony for sea for two months immediately after laying.

LAYING   At any hour of day or night. At Pte Géologie, average date of first egg, 2 May (27 Apr.–5 May; 12) (Prévost 1961; Arnaud 1964; Guillard & Prévost 1964; Mougin 1966; Birr 1968; Isenmann & Jouventin 1970; Bougaeff 1974); of last egg, 7 June (29 May–12 June; 4) (Prévost 1961; Mougin 1966; Isenmann 1971). Thus, c. 35 days between first and last laid clutches and mean date of laying c. 20 May. Similar at other colonies at equivalent latitudes; 1 month later, c. 20 June at more southerly colonies (J.C. Boyd).

INCUBATION   By male alone. If female retains egg after laying for a few hours, she protects it against cold rather then broods it fully. Thus, male fasts for c. 6 weeks of pair-formation plus c. 9 weeks of incubation. INCUBATION PERIOD.: 64.4 days (1.4; 62–67; 20) (Prévost 1961). At Pte Géologie, hatching reported on average from 5 July (2 days; 1–8 July; 12) (Bougaeff 1974); somewhat later at southerly colonies. Addled eggs may be incubated into Aug., even Sept. (Mougin 1966). Adults do not recognize their own egg nor help chicks to break out of shells except by fortuitous movements, which may help to break the shell.

YOUNG   Semi-altricial, nidicolous. Hatched with pale-grey down, black on head and two white spots round eyes. Teleoptile appears at beginning of Nov. and complete by beginning Dec. Brooded by male for c. 10 days; male then leaves for sea after fasting for average 115 days (105–134; 133; Isenmann 1971) and losing c. 40% of weight (Groscolas 1982). Female then broods for 24 days and is relieved by male for another 7 days. Thereafter chicks form crèches for about last 100 days before departure. Both adults feed chick and only their own. First meal given by male at end of his fast before female returns; this is an oesophageal secretion, rich in protein and similar to pigeon's milk (Prévost & Vilter 1963); later meals entirely of marine organisms. Two more meals given during brood-stage, one by each sex; then each sex provides 6–12 meals during crèche-stage, before departure (Isenmann 1971). All meals by incomplete regurgitation; bouts of feeding may take several days, especially for young chicks, providing several kilograms of food in total.

GROWTH   Weight at hatching average 315 (250–385; 24) (Prévost 1961) or about 70% of fresh-egg weight. Increase in weight during brood-stage slow, improves later: 35g/day, Aug.; 95 g/day, Sept.; 190 g/day, Oct. (Mougin 1966). Maximum weight just before departure, 10–15 kg or 45% of average adult weight (Jouventin & Mougin 1981); on departure, all dimensions shorter than adult, except length of flipper (Prévost 1961).

FLEDGING TO MATURITY   After moult, chicks leave voluntarily at any hour of day or night, but may sometimes be carried away by early break-up of sea-ice. At Pte Géologie, average first departures 5 Dec. (7 days; 30 Nov.–18 Dec.; 8) (Bougaeff 1974); somewhat earlier in southerly colonies where fledging period of chicks apparently shorter than in north (Boyd *et al.* 1970). Completely independent of adults on departure and thus heavy mortality of immatures. Annual moult takes place anywhere, sometimes in natal colony. First return to colony aged 4.2 years (1.5; 1–10; 260); first breed at 5.2 years (1.0,3–9, 124) (Mougin & van Beveren 1979).

SUCCESS   At Pte Géologie, during 16 breeding cycles between 1952 and 1978, when colony in equilibrium, 87 731 eggs laid; 75 745 hatched (13.7% failed); 25.4% of chicks died during fledging period; thus total mortality 35.6% and total fledging success 64.4%. During same period, 209 of 1092 chicks, banded before departure, alive after one year; thus survival of first-year immatures 0.1914. Survival rate of adults 0.9509, annual rate of mortality 0.0491 and mean longevity 19.9 years (Mougin & van Beveren 1979). Loss of eggs mostly by desertion in first few days after laying, by infertility or by imperfect incubation; loss of chicks mostly in Sept. just after formation of crèches, when chicks are fed at rather long intervals and not protected by parents against cold snaps, thus becoming vulnerable to climatic dangers and to alimentary disorders (Jouventin 1975). Under-nutrition important cause of loss of chick. Breeding success may depend on annual vari-

ation in ice conditions, especially in colonies far from sea; when ice break-up or opening of leads and cracks delayed, adults must travel farther or use inferior fishing grounds. At Pte Géologie, mortality of chicks highest when open water far from colony (Jouventin 1975). Topographical and climatological factors can affect colonies. The possible extinction of colony on Stancomb-Wills Promontory probably caused by disappearance of glacier tongue, which sheltered birds against winds. PREDATORS. Not important before fledging, except perhaps giant-petrels *Macronectes* spp, because chicks defend themselves when crèched. At sea, adults and immatures preyed on by Leopard Seals *Hydrurga leptonyx* and Killer Whales *Orcina orca*. Probably not much affected by human activities; yet decline of colony at Pte Géologie may have been caused by disturbancies at Dumont d'Urville, though retreat of Astrolabe Glacier, exposing colony to storms that break up sea-ice and cause significant loss of chicks, also perhaps involved (Jouventin *et al.* 1984). Similar fluctuations noted at C. Crozier in absence of man (Todd 1980).

PLUMAGES

ADULT   In fresh plumage: HEAD AND NECK. Feathering of head, black (89); extending from hindneck in upwards crescentic shape, then abruptly downwards from auricular area to lower throat. Feathers, dense and short; cover interramal space and base of upper mandible, ending at base of groove of culminicorn and latericorn. Large, almost circular, patch of white feathers on side of neck, continuous with rest of neck, joining at mid-point; continuity occurs in narrow margin between separation of lower throat and moderately broad band of black-brown (119) feathers, extending from axillary area to the neck. Rest of neck, pale yellow (157) merging to white on ventral side. At sides of neck, in incomplete circular patch, small patch of orange-yellow (18) feathering in auricular area, gradually fades to pale yellow (157) down neck. Orange-yellow (18) auricular feathering sometimes extends along border of black (89) throat, but less bright. Nape to lower neck, dark brown (121) with tips of feathers pale grey (86) to light blue-grey (88); rachis broad and black (89) at tip. UPPERPARTS. Mantle to rump, similar to nape; on back, tips of feathers, light blue-grey (88). Upper tail-coverts, black-brown (119), tips of feathers, pale grey (86). In worn plumage, in pre-moult, feathers on dorsum, dark brown (121); most grey tips lost. TAIL. Rectrices, black-brown (119). UPPERFLIPPER. Feathering on dorsal side of flipper, short, well ordered in rows; scale-like anteriorly, longer posteriorly. At base of flipper, feathers black-brown (119) with pale-grey (86) tips. Anteriorly, feathers black-brown (119) with narrow light blue-grey (88) tips; towards posterior, tips more prominent. Last row of feathers on flipper, white. UNDERPARTS. Upper breast to under tail-coverts, white. Feathers in vent area and thighs, long; feathers extend to base of outer toe. Ventral portion of thighs, white; dorsal side, as for rump. Sharp demarcation at border of dorsum and venter along flanks; inward progression of white adjoining abdomen in lower flank area. In this area, at border, feathers have shaft streaks of black-brown (119); tips of feathers either white or light blue-grey (88). UNDERFLIPPER, white apart from last two feather-rows; dark brown (121) with white tips. Adult plumage acquired at 18 months. Concealed parts of feathers at nape: rachis white at base; rami, pale dark-brown (121) basally; visible in moult and dislodged feathers. Similarly, from mantle to rump: rachis light grey-brown (119C) at base merging to brown (119B). Rami at base, light grey-brown (119D).

DOWNY YOUNG   Protoptile short. HEAD AND NECK. Entire head from hindcrown, including crown, frons to gape, extending to chin and interramal space, black (89); borders with rest of white down on head, forming 'mask'; including throat, most of lores, over eyes and ears. Eyes and ears surrounded by shorter white down. Long narrow strip of black (89) down, extending from hindcrown to base of flipper, black (89). At lower neck, on ventral side, black (89) down extends across neck, almost joining at centre; separated by small patch of light-grey (85) down. Remaining sides of neck and nape, pearl grey (81). UPPERPARTS. Dorsum, white, from mantle to rump; silky and hairy. TAIL.-tuft, black-brown (119) at base, paler brownish-grey (79) at tip. UPPERFLIPPER. Dorsal surface of flipper, light grey (85) with thin white posterior edge. UNDERPARTS., as dorsum. UNDERFLIPPER., white.

Teleoptile similar to protoptile; down differs in being thicker and hairy, light grey (85) with white tips, on dorsum and venter. Rudimentary tail, black-brown (119) with hair-like tips. In older chicks, down on crown, dark brown (121); venter, light grey-brown (119C). Teleoptile begins to appear at beginning of Nov.; complete in *c.* 1 month (Prévost 1961).

JUVENILE   Similar to adult, differences described here only. Head, black-brown (119), paler round eyes and interramal space. Chin and throat, white. Crescentic shape near auricular area, less defined with little abrupt downwards
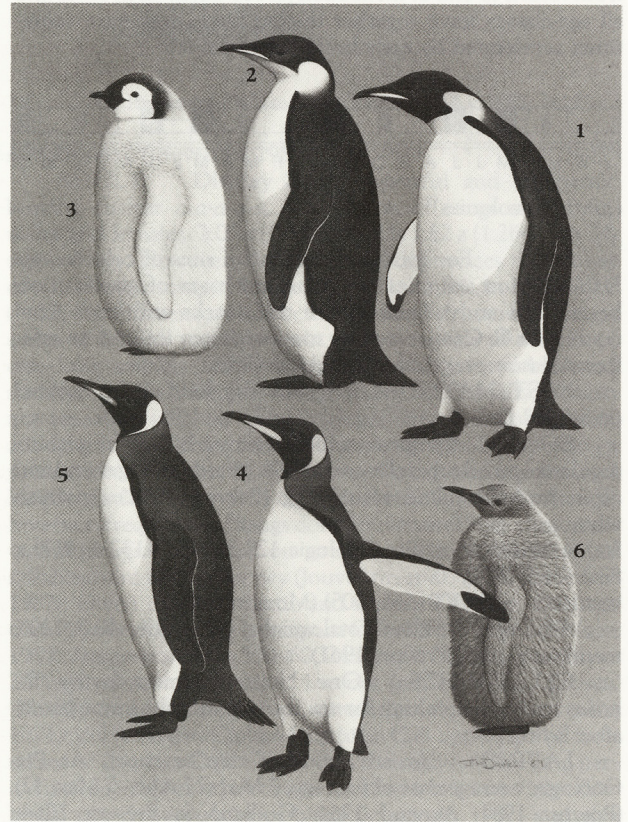

Plate 7

Emperor Penguin *Aptenodytes forsteri*
1. Adult
2. Juvenile
3. Downy young, mesoptile

King Penguin *Aptenodytes patagonicus*
4. Adult
5. Juvenile
6. Downy young, mesoptile

marking. Broad band of black-brown (119) feathering from axillary area less prominent. As a consequence, margin of white feathering, broader. Orange-yellow (18) marking absent in auricular patch; feathering white, with pale yellow (157) wash, merging to brownish-grey (80) near nape. Following post-juvenile moult, indistinguishable from adult at *c.* 18 months (Prèvost 1961).

ABERRANT PLUMAGES   Albino chicks recorded (Makushok 1959).

BARE PARTS

ADULT   Iris, dark brown (c219). Upper mandible, grey-black (82); lower, grey-black (82) with pink (108D) extending two-thirds of length, surrounded distally, with thin light violet (170D) strip; rest, light blue-grey (88). Legs and feet, grey-black (82).

DOWNY YOUNG   Iris, black-brown (119). Upper and lower mandibles, grey-black (82); egg-tooth, white. Legs and feet, grey-black (82).

JUVENILE   Similar to adult; differs in two-thirds of lower mandible being dull pink (5).

MOULTS

ADULT POST-BREEDING   Moult occurs when rearing of chicks complete (Groscolas 1978). Breeders moult

Dec.–Feb. (Falla 1937; Groscolas 1978). Moult season, Nov.–Jan.; breeders, non-breeders, juveniles moult during this period (Le Maho 1977). Actual dates of first appearance of moult, given as 23–28 Nov., 1 Dec. and 11 Dec.(Prèvost 1961; Pryor 1964; Kamenev 1967). Duration of moult 30–40 days (Prèvost 1961; Le Maho *et al.* 1976; Le Maho 1977). In captivity, partial moults varied from 16 to 22 days, and full moult of 32 days; sequence of moult recorded: postero-ventral region, then irregularly until dorso-anterior regions last (Davis 1945). Davis (1945) records partial moult involving ramphotheca of lower mandible. Sequence of moult begins with appearance of new rectrices, fading of plumage; last to go are feathers of nape and lower back (Le Maho *et al.* 1976; Groscolas 1978). Further details of sequence given in Wilson (1907). Falla (1937), records sequence as: tail, lower back; thighs, flippers, rest of back, breast and head. Full details of feather growth, synthesis and sequence during moult, given in Groscolas (1978).

POST-JUVENILE   Moult season: Nov.–Dec. Lower sides and tips of flippers and base of tail first to change (Pryor 1964). First sign of moult of large chicks, 10 Nov. (Makushok 1959). Moult in old chick, noted as starting on flippers and tail (Falla 1937). Juvenile plumage attained at *c.* 150–170 days (Watson 1975). Additional details given in Arnaud (1964).

MEASUREMENTS   (1) Skins from various localities, adult and subadult combined; data from Falla (1937).

		MALES	FEMALES
FLIPPER	(1)	368.0 (9.27; 360–385; 5)	355.0 (23.23; 310–375; 5)
BILL	(1)	82.0 (6.84; 71–92; 5)	81.4 (5.67; 74–87; 5)
TOE	(1)	100.7 (3.96; 96–107; 4)	103.7 (2.16; 100–105; 4)
TAIL	(1)	69.6 (15.92; 50–89; 3)	70.5 (20.32; 40–97; 4)

Unsexed birds (2) Data from Falla (1937).

		UNSEXED
FLIPPER	(2)	355.8 (14.55; 330–380; 9)
BILL	(2)	75.4 (4.00; 70–82; 9)
TOE	(2)	98.3 (6.23; 90–105; 3)
TAIL	(2)	85.3 (6.12; 3) 78–93

Full details of growth rates of chicks, given in Wilson (1907) and Stonehouse (1953).

WEIGHTS   Marked seasonal difference; also varies between moulting and non-moulting birds. During breeding season, males fast for 105–134 days (n=133; Isenmann 1971); 115–120 days (Goldsmith & Sladen 1961; Groscolas 1982); females fast for 45 days (Groscolas 1982). In Terre Adélie, in moulting birds, mean weight of adult males, 38.2 kg (n=9) and females 29.5 kg (n=7) at beginning of breeding. At end of breeding fast, males weigh 22.8 kg (n=9) and females 23.1 kg (n=7), representing reduction of 40.5% and 21.8% for males and females respectively (Groscolas 1982). Loss of 46.5% of weight recorded in juveniles (Groscolas 1978). Full details of daily loss of weight in Le Maho *et al.* (1976) and Groscolas (1978). For further experimental comparisons of weight in moulting and non-moulting birds, see details in Le Maho *et al.* (1976) and summary presented in Croxall (1982). Further seasonal data and comparison of sexes in Mougin (1966). De-
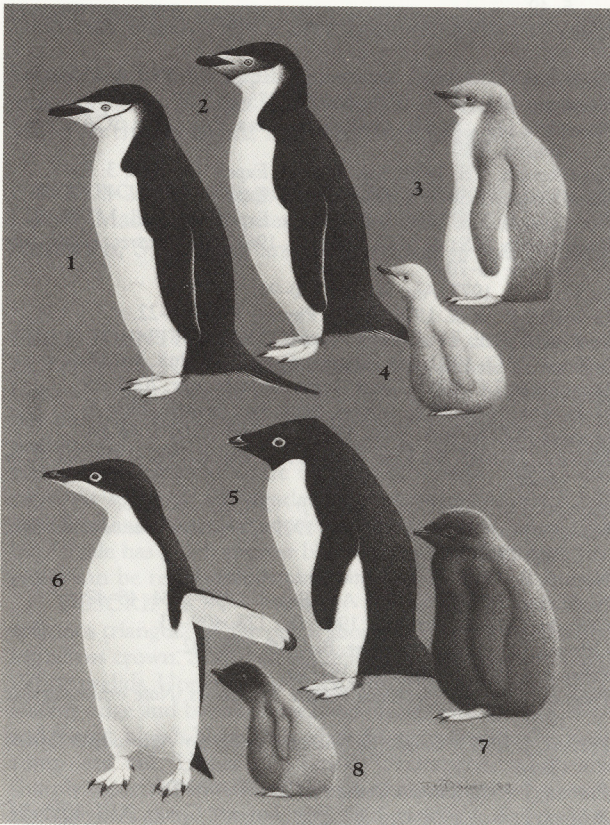

Plate 8

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

tails of changes of weight in chicks in Wilson (1907), Stonehouse (1953), Prévost (1961), Pryor (1964), Guillard & Prévost (1964), Mougin (1966) and Jouventin & Mougin (1981).

STRUCTURE   Flightless. Largest penguin. Flipper, hard and bony, long, broad at base. Feathering of body dense, strongly lanceolate; rachis broad and flattened at tips; imparts glossy appearance. About 18 rectrices, t1 longest; assessment of configuration of rectrices difficult; upper tail-coverts of equal length. Rachis of tail, broad, stiff basally; rounded on dorsal side, concavely ridged, shallow on ventral. Tail, rectangular. Bill, long, slender and decurved. Legs, very short; hexagonal or pentagonal scutes on tarsus and toes; feet webbed; extraneous fold of skin along outer edge of inner toe; slight on either side of middle. Pads of soles thick. Claws, long, thick and curved. Outer toe c. 70% of middle, inner c. 60%, hind very reduced, c. 9%.

AGEING   Age of chicks can be determined on growth-curve analysis (Le Resche et al. 1970); derived from study of known-age chicks from Wilson (1907) and Stonehouse (1953).

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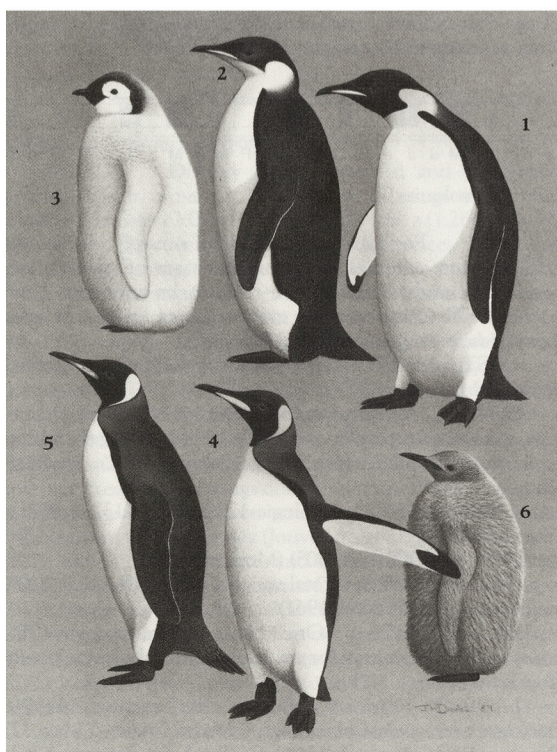
Volume 1 (Part A), Plate 7

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