

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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Aptenodytes papua Forster, 1781, *Comment. Phys. Soc. R. Sci. Götting.* 3: 134, 140, Pl. 3 — Falkland Islands.

The generic name is compounded of the Greek *πυγών* (elbow) and *οκέλος* (leg) i.e. elbow legs. The specific name was a mistake on the part of Forster who applied it to birds taken in the Falkland Is because Sonnerat had previously incorrectly reported the species from New Guinea. The word *papua* is Malayan for *curly* but the species has no feature to which this could reasonably be applied.

OTHER ENGLISH NAMES Johnny Penguin, Johnny, and, in error, Rockhopper and Jackass.

Gentoo in various spellings means a pagan inhabitant of Hindustan, opposed to Mohammedan; a Hindoo; one speaking Telugu (OED) and is of Anglo-Indian and Portugese origin. No reason for applying the word to this penguin has ever been suggested.

POLYTYPIC Nominate *papua* in Subantarctic Zone on Marion, Prince Edward Is, Iles Crozet, Iles Kerguelen, Heard, Macquarie, Staten, Falkland Is, S. Georgia; *ellsworthii* Murphy, 1947, in Antarctic Zone on S. Sandwich, S. Orkney and S. Shetland Is and on Antarctic Pen. to about 65°S.

FIELD IDENTIFICATION Length 75 cm (Macquarie I.); flipper 190–270 mm; weight male 5.5 kg, female 5.0 kg. Tall black-and-white penguin of Subantarctic, with bright-orange bill and feet. Head black with prominent triangle of white feathers above each eye, meeting across crown. White ring round eye. Scattered white feathers on crown, cheeks and nape. At sea, look for slender bright-orange and black bill, dark head and diagnostic white triangles over eyes. Sexes alike but female has much shorter bill. No seasonal plumages. Juveniles can be recognized.

DESCRIPTION ADULT. Head, black with conspicuous triangular white patch above each eye, usually meeting across crown. Scattered white feathers on head and nape. White eyelids. Upperflipper black with thin white band along leading-edge and broad white band along trailing-edge. Back and throat, bluish-black with white fringe extending between rump and tail. Upper tail, black. Underparts, white and sharply separated from black throat. Underflipper white with blackish area at tip. Dorsum appears browner in worn plumage. Bill, orange-yellow to coral-red on sides with black culmen and tips of mandible. Iris, brown. Feet, pale yellow to deep orange. Variation in colours of bill and feet appears to be genetic and not varying with age, sex or season (Downes *et al.* 1959). **JUVENILE.** Duller bill than adult. Also, white bar over crown narrower and duller (Bagshawe 1938); separated from eye by white flecking (Downes *et al.* 1959). All birds that have

white head bar not reaching eye are juveniles (Trivelpiece *et al.* 1985); but in some juveniles, white patch continues to eye as in adults (Williams 1988). Eyelids usually dark but some juveniles have white eye-ring like adults (Downes *et al.* 1959). Mottled grey chin and throat.

SIMILAR SPECIES Unmistakable; cannot be confused with other penguins in its normal range. Distinguished from **Adelie Penguin** *Pygoscelis adeliae* by bright orange bill and conspicuous white eye-patches.

Circumpolar in Subantarctic zone. Usually go to sea in groups early in day; later in day, more often singly; birds wade into water until flippers half submerged, fall over and then swim first 10–20 m under water, after which surface and wash for several minutes (rub bodies with flippers while twisting and turning over) before departing; others may stand on beach for several minutes before leaving. On return, porpoise up to 10–20 m offshore and then swim about on surface, surveying area before diving and swimming ashore quickly in incoming wave. Bill used as support to rise and move out of water. Once out, stop to swallow and shake head before moving away from sea to preen. If caught by wave, they go out with it and come in on next wave. On icy coasts, they leap out of water onto ice in similar fashion to Adelie and Emperor *Aptenodytes forsteri* Penguins. May also jump out of water onto rock shelves. All birds preen after landing. Walk with flippers raised and behind body at 10–90° to long axis of body; tail held between 15°

below horizontal to 60° above horizontal; body sways from side-to-side; speed 1.5–3.4 km/h. Tobogganing common when fleeing, on snow or when moulting; in same manner as other penguins, on breasts, using flippers as oars while paddling with feet; uncommon at Marion I. because there is no snow. Also hop and jump over obstacles, stones and ledges. Preen by scratching with bill or rubbing head along flipper; oiling done after coming ashore or at nest-site. Oil-gland nibbled and oil distributed over flippers by nibbling with bill; then on head and body by rubbing with flippers and bill. At sea, more than 90% of time spent porpoising below surface; only rarely swim at surface, with most of body underwater and only head, top of back and tail showing. Breed in small to large colonies. Utter braying or trumpeting calls on land at colonies; hiss when threatened; also give sharp contact call at sea.

HABITAT Marine; circumpolar in subantarctic and Antarctic waters; over 80% birds S of Antarctic Convergence (Stonehouse 1985), although occur over wide latitudinal range from 45 to 65°S. Avoid pack-ice and continental coasts, except near Antarctic Pen. Usually remain near breeding islands throughout year. When breeding, thought to forage inshore, as main prey occurs in shallow water (Williams 1980a; Croxall & Prince 1980; LaCock *et al.* 1984; Trivelpiece *et al.* 1986, 1987). At S. Georgia, probably associated with inshore kelp beds in depths <30 m (Croxall & Prince 1980), but also observed over banks 75 km from shore (Murphy).

Breed on ice-free ground on Antarctic Pen. and on Antarctic and subantarctic islands. Colonies inland or coastal, on beach terraces, coastal flats, valleys, slopes, low headlands, inland hills, knolls, ridges and cliff tops (Murphy; Falla 1937; Rand 1954; Downes *et al.* 1959; Despin 1972; Muller-Schwarze & Muller-Schwarze 1975; White & Conroy 1975; Robertson 1986). Breeding distribution on Macquarie, Marion and Prince Edward Is may be determined by underwater topography, with colonies concentrated near shallow feeding areas (Robertson 1986; Adams & Wilson 1987). Moults ashore at colonies (Downes *et al.* 1959).

Range may have extended and numbers increased in last few decades, perhaps because whaling has increased availability of krill (Conroy 1975), though populations also believed to have remained stable since 1950 (Croxall & Kirkwood 1979).

DISTRIBUTION AND POPULATION Circumpolar; pelagic, mostly confined to region of winter pack-ice. Breed Antarctic Pen., and subantarctic islands of South Atlantic, Indian and Pacific Oceans. Vagrant to Aust. and NZ.

Inhabit Antarctic and subantarctic regions from continental coast to just beyond n. limit of pack-ice. Range at sea poorly known; n. breeding populations may remain at or near colonies throughout year (Oliver; Matthews 1929; Bennett 1926; Vallentine 1924) while s. birds from area between S. Orkney Is and Peterman I. migrate though a few may remain in winter as far S as open water can be found (Brown *et al.* 1906; Valette 1906; Gain 1914; Trivelpiece *et al.* 1987). In winter, accidental to South America, reaching coast of Argentina as far as 43°S; vagrant to Aust. and NZ.

AUST. Four records, all Tas.: Eaglehawk Neck, 1925 (probably Mar.) (Fletcher 1926; Alexander 1926); Marion Bay, 12 May 1975 (Tas. Bird Rep. 1975); Trial Harbour, 30 Dec.

1977 (Aust. Atlas); South Cape Bay, 8 Jan. 1989 (Tas. Bird Rep. 1989).

NZ First mainland record, single, St Kilda Beach, Otago Pen., SI, 22 Sept. 1970 (Darby & Wright 1973); Tiwai Pt, Bluff, Southland, 1 Nov. 1970 (CSN 19) and said to have occurred Banks Pen. but without further details. Also recorded Antipodes I., Nov. 1978 (P.J. Moors); Campbell I., single birds, 29 Dec. 1964, and 9 Jan., 3 Mar., 8 Aug. 1965, possibly same individual (Kinsky 1969), 26 Dec. 1985 (P.J. Moors); single, Snares Is, 27 Dec. 1987 (CSN 34).

BREEDING Circumpolar; colonies located between 65°11'S and 46°S; on Antarctic Pen. and subantarctic islands.

Antarctic Pen.: 60–70 colonies on Petermann I., Pléneau I., Glandaz Pt, Loubat Pt, Humphries Heights, Port Charcot, Weincke I., Truant I., Pursuit Pt, Doumer I., Port Lockroy, Damoy Pt, Joubin I., Gerlache I., Quinton Pt, Anvers I., Bryde I., Waterboat Pt, Useful I., Ketley Pt, Beneden Head, Rongé I., Cuverville I., Danco I., Neko Harbour, Gerlache Str., Sternneck I., Charles Pt, C. Spring, Skottsberg Pt, Mikkelsen Harbour, Trinity Pen., Joinville I., Patella I. Total population about 20 000 pairs; size of colonies averages about 450 (50–1500) (Poncet & Poncet 1987; Croxall & Kirkwood 1979; Elliot *et al.* 1978).

Prince Edward Is: more than 15 colonies on Marion and Prince Edward Is, with population of 1500–2000 pairs (Williams *et al.* 1979).

Iles Crozet: 27 colonies on Iles de la Possession, de l'Est, aux Cochons with population of c. 5000 pairs (Jouventin & Weimerskirch in press; Jouventin *et al.* 1984; Derenne *et al.* 1976; Voisin 1984).

Iles Kerguelen: 30 000–40 000 pairs (Weimerskirch *et al.* 1989).

Heard I.: 16 colonies, with c. 10 000–16 000 pairs (Downes *et al.* 1959)

Macquarie I.: 53 colonies with 4700 pairs (Robertson 1986).

S. Shetland Is: c. 25 colonies on Nelson, King George, Ardley, Snow, Low and Elephant Is, with population of 20 000–24 000 (Croxall & Kirkwood 1979; Shuford & Spear 1987)

S. Orkney Is: 6–8 colonies on Coronation, Signy, Powell, Laurie, Michelsen and Christoffersen Is with population of 2500–3600 pairs (Poncet & Poncet 1985; Croxall & Kirkwood 1979).

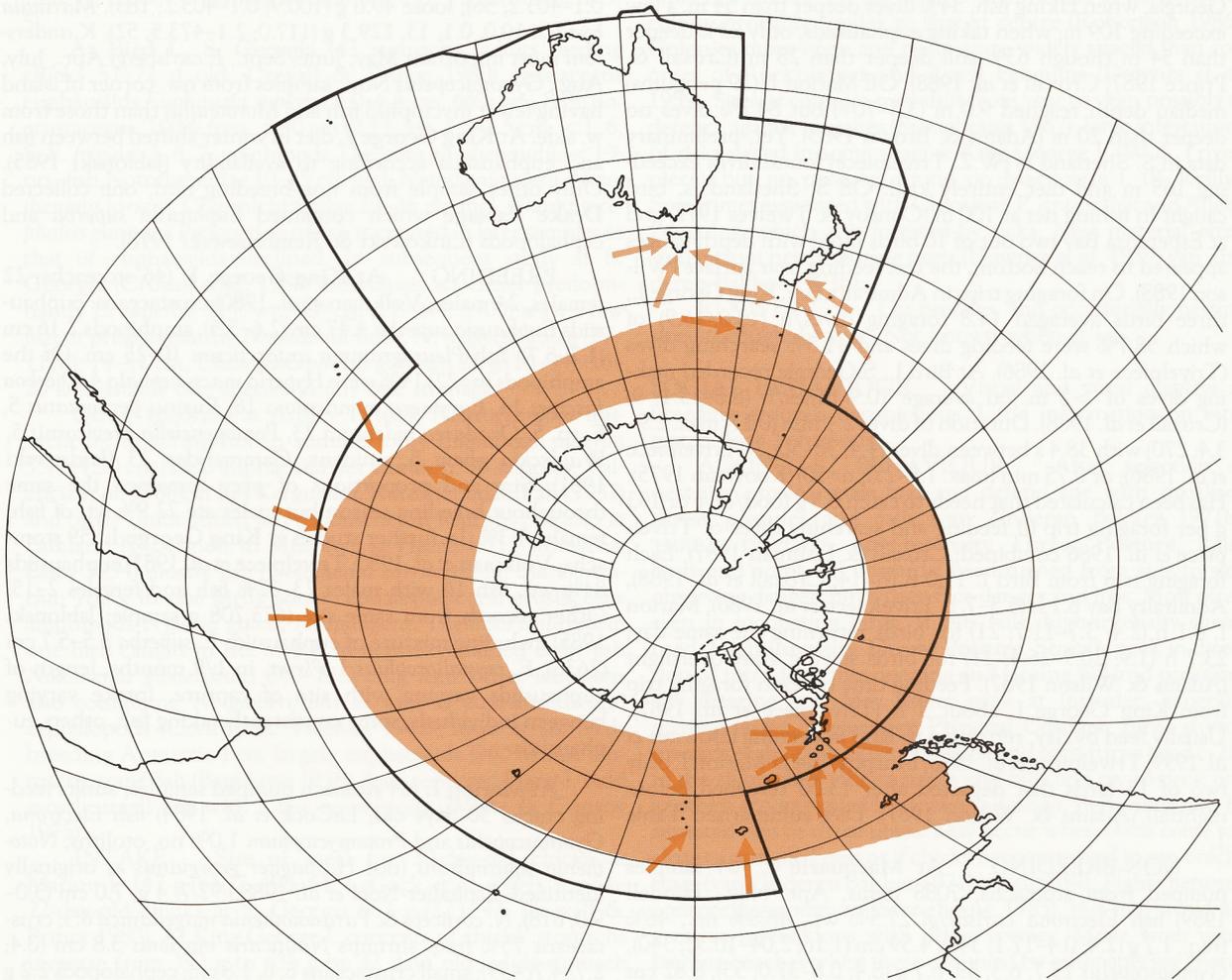
S. Georgia: 180 colonies with 80 000–100 000 pairs (Croxall *et al.* 1984a; Jouventin & Weimerskirch in press).

S. Sandwich Is: 6 colonies with 2000 pairs (Croxall *et al.* 1984a).

Extralimital: c. 85 colonies on Falkland Is with 110 000–120 000 pairs (Croxall *et al.* 1984b).

POPULATION Total population, estimated 260 000 pairs (Robertson 1986). Status satisfactory; numbers stable or increasing slightly, not to same extent as Adie and Chinstrap *P. antarctica* Penguins (Volkman & Trivelpiece 1980). Exploitation by egg collectors and for rendering into oil caused decline on Falkland Is. Exterminated on some islands where formerly in large numbers (Croxall *et al.* 1984b). Sensitive to human activity; declined on Iles Kerguelen after permanent base constructed (Jouventin *et al.* 1984). Population on Macquarie I. probably stable (Rounsevell & Brothers 1984).

MOVEMENTS Essentially sedentary at most breeding



sites, though numbers at colonies lower during winter.

DEPARTURE Usually absent from actual colonies at Signy I., S. Orkney Is, after Mar. (Rootes 1988) and most adults appear to depart Heard I. in Apr. after moult, immatures leaving a month earlier (Downes *et al.* 1959).

NON-BREEDING Some birds present throughout year at most colonies including Iles Crozet (Despin 1972), Iles Kerguelen (Paulian 1953), Heard I. (Downes *et al.* 1959), S. Shetland Is (Trivelpiece *et al.* 1983; Jablonski 1987), S. Georgia (Stonehouse 1985), Antarctic Pen. (Bagshawe 1938). At Iles Kerguelen, banded juveniles found at nest sites 6 months after fledging (Paulian 1953). However at least some birds move, numbers at King George I. declining to 53–60% of breeding population in Apr.–May and 14–24% from mid-May to mid-July (Jablonski 1987). Watson (1975) has suggested most birds from Antarctic Pen. move N during June and July when numbers at colonies lowest (Bagshawe 1938); an immature appeared in NZ in Sept. (Darby & Wright 1973), and vagrants have reached Campbell I. in Dec.–Mar. and Aug. (Kinsky 1969), and Tas. in Jan., Dec., May and probably in Mar. (Alexander 1926; Fletcher 1926; Tas. Bird Reps 1975, 1989; Aust. Atlas).

RETURN Adults return in large numbers to Ile de la Possession, Iles Crozet, late June–early July (Despin 1972); to

Iles Kerguelen (Paulian 1953), Heard I. (Downes *et al.* 1959) and Antarctic Pen. (Bagshawe 1938), mid-late Aug.; to Signy I., 28 Sept. (10.8 days; 3 Sept.–28 Oct.; 13 years) (Rootes 1988); and to King George I., 7–25 Oct. (Jablonski 1987); though at all sites numbers build up gradually over several months.

BREEDING Movements during breeding season local as most feeding in inshore waters (Williams 1980a) with range of 24–35 km (Adams & Wilson 1987; Croxall & Prince 1987; Trivelpiece *et al.* 1987). In some areas (Admiralty Bay; Jablonski 1985; Trivelpiece *et al.* 1986; Bird I., S. Georgia; Croxall *et al.* 1984c) usually travels <10 km. At Marion I. travelling speed 7.9 km/h (1.5; 3.9–10.6; 53) (Adams & Wilson 1987) with length of foraging trip depending on colony: at Kildalkey, median length N, 13.8 km (0.64–103.0; 19), at Archway Bay and Ship's Cove, 30.7 (1.6–96.7; 19), 82% of all trips <40 km. On foraging trips in Admiralty Bay, King George I., three birds averaged 4.2 km/h (3.1–5.3; straight line distances) (Trivelpiece *et al.* 1986).

FOOD Proportions of fish and euphausiids vary with locality; euphausiids tend to predominate in diet near Antarctica but fish increasingly prevalent in marginal breeding areas N of Antarctic Convergence. **BEHAVIOUR.** Takes food by pursuit-diving, depth dependent on type of prey. Off S.

Georgia, when taking fish, 54% dives deeper than 54 m, a few exceeding 109 m; when taking euphausiids, only 23% deeper than 54 m though 63% still deeper than 28 m (Croxall & Prince 1987; Croxall *et al.* 1988). Off Marion I. (19 penguins) median depth reached 9.0 m (3.5–70+) but 84.2% dives no deeper than 20 m (Adams & Brown 1983). Yet, preliminary data in S. Shetland Is (W.Z. Trivelpiece) found dives exceeding 165 m and diet entirely krill. Off S. Shetland Is, bird caught in fishing net at 100 m (Conroy & Twelves 1972) and at Esperanza Bay two out of 10 birds fitted with depth gauges appeared to reach bottom, the rest feeding near surface (Wilson 1988). On foraging trips in Admiralty Bay, King George I., three birds averaged 14.8 foraging dives/h (13.0–16.9) of which 58.7% were feeding dives and 41.3% searching dives (Trivelpiece *et al.* 1986). At Bird I., S. Georgia recorded making dives of >2 m, on average 10.9 times/h (8.8–13.1; 9) (Croxall *et al.* 1988). Duration of dives 2.1 min (0.17; max. 2.9–3.4; 270) with 38.4 s between dives (4.4; 30–50; 7) (Trivelpiece *et al.* 1986); or 0.75 min (max. 1.5–2.0; n=50) (Kooymann 1975). Has been calculated that needs to catch 6.5 g food/dive or 193 g per foraging trip (if feeding and searching dives of Trivelpiece *et al.* 1986 combined; Croxall & Lishman 1987). Each foraging trip from Bird I. 11.0 h (n=14; Croxall *et al.* 1988), Admiralty Bay 6.1 h (5.5–7.1; Trivelpiece *et al.* 1986), Marion I. 8.1 h (2.4; 3.7–11.7; 21) for birds returning the same day; 23.7 h (1.9; 20.9–26.4; 11) for birds staying away overnight (Adams & Wilson 1987). Feeding time on each foraging trip from King George I. about 3 h (Trivelpiece *et al.* 1987). Usually feed by day, returning to land in evening (Downes *et al.* 1959; Trivelpiece *et al.* 1986; Murphy) but at Marion I. only two of 13 birds that departed after 13:00 returned before nightfall (Adams & Wilson 1987). Diet summarized Table 1.

NON-BREEDING At **Macquarie I.** (64 samples pumped from stomachs, 7088 items, Apr.–Nov.; Hindell 1989) fish *Electrona carlsbergi* 27.5% wt., 48.8% no., 48% freq., 1.7 g (2.4; 0.4–17.1; 340), 4.59 cm (1.16; 2.04–10.32; 340), *Gymnoscopelus* 15.7, 6.3, 39, 6.7 g (8.4; 0.8–37.0; 53), 8.82 cm (3.34; 4.69–18.08; 53), *Krefflichthys anderssoni* 15.1, 35.0, 59, 1.3 g (1.9; 0.1–6.7; 376), 3.75 cm (1.52; 1.24–7.50; 376), *Protomyctophum* 0.8, 1.7, 9, *Magnesudis prionosa* 0.4, <0.1, 3, *Zanclorhynchus spinifer* 0.9, 0.1, 6, *Notothenia rossii* 2.0, 0.2, 6, *Paranotothenia magellanica* 18.4, 2.3, 28, 23.8 g (27.9; 0.1–100.0; 23), 8.48 cm (5.06; 0.76–18.00; 23), *Harpagifer georgianus* 0.5, 0.7, 13, 2.2 g (1.4; 0.1–5.3; 37), 4.67 cm (1.19; 2.64–6.41; 37), unident. fish 0.3, <0.1, 10; crustaceans: euphausiids <0.1, 1.1, 13, amphipods *Cylopus lucasii* <0.1, 0.3, 13, Gammaridea <0.1, 2.3, 8, unident. amphipods <0.1, 0.1, 6; cephalopods *Moroteuthis* 8.6, 0.9, 45, with flesh 27.9 g (88.8;

0.1–403.2; 56); loose 49.6 g (100.9; 0.1–403.2; 183), *Martialia hyadesi* 10.0, 0.1, 13, 229.3 g (117.0; 2.1–473.5; 52). *K. anderssoni* most important May, June, Sept., *E. carlsbergi* Apr., July, Aug., *Gymnoscopelus* Nov., samples from nw. corner of island having fewer myctophid fish and *Moroteuthis* than those from w. side. At **King George I.** diet in winter shifted between fish and euphausiids according to availability (Jablonski 1985). Only other sample from non-breeding bird, one collected **Drake Passage** which contained *Euphausia superba* and cephalopods (Linkowski & Rembiszewski 1978).

BREEDING At **King George I.** (46 stomachs, 22 females, 24 males; Volkman *et al.* 1980) crustaceans: euphausiids *Euphausia superba* 4.47 cm (2.6–5.5), amphipods 2.16 cm (1.2–5.7); fish *Pleurogramma antarcticum* 10–25 cm. Of the amphipods (n=22) 14% were *Hyperia macrocephala* 4, *Djerboa furcipes* 14, *Eurymera monticulosa* 18, *Eusirus perdentatus* 5, *E. sp.* 5, *Oradarea bidentata* 23, *Pontogeneiella brevicornis* 5, *Waldeckia obesa* 5, unident. Gammaridea 23 (Jazdzewski 1981). Size and proportions of prey remained the same throughout breeding season but males ate 22.9% wt. of fish, females 7.3%. In further studies at **King George I.** (59 stomachs; Volkman *et al.* 1980; Trivelpiece *et al.* 1983) euphausiids 84% wt., fish 16 with males 23–32% fish and females 2–15. Other records from same site (623,708 g sample; Jablonski 1985) including mixture of euphausiids *E. superba* 3.5–5.7 cm (2636), *E. crystallorophias* 1.5% wt. in 1/9 months, length of euphausiids varying with site of capture, intake varying between individuals, some consistently taking fish, others euphausiids.

At **Marion I.** (64 stomach pumped samples, adults feeding chicks 30 days old; LaCock *et al.* 1984) fish *Electrona*, *Gymnoscopelus* and *Protomyctophum* 1.0% no. otoliths, *Notothenia squamifrons* (not *Harpagifer georgianus* as originally identified; Espitalier-Noel *et al.* 1988.), 92.7, 4 g, 7.0 cm (3.0–9.0; 618), *N. coriiceps* & *Paranotothenia magellanica* 6.3; crustaceans 75% freq. shrimps *Nauticaris marionis* 3.8 cm (0.4; 2.7–4.7; 439); small crustaceans 6, 6, 1.8 cm; cephalopods 2.2 g (1.9; 0.7–7.3; 11); Teuthoidea 64% no. including *Kondakovia longimana*, Octopoda 36; also gastropods 8% freq. Change in faeces colour from red to white had suggested diet at Marion I. changed from crustaceans to fish in Oct. (Williams 1981) but, in some years, fish certainly predominate by Sept. (LaCock *et al.* 1984). In early Sept. (27 stomach pumped samples; Adams & Wilson 1987) samples usually homogeneous for any food type: 11 contained only *N. marionis* 3.19 cm, 10 only *N. squamifrons* 7.49 cm and two *Euphausia vallentini* 2.45 cm with the other four samples mixed. Samples containing only *N. marionis* were collected from birds travelling 8.8 km (6.4–

Table 1. Diet of Gentoo Penguin.

	% wt.						% no.			% freq.				
	1	2	3	4	5	6	1	2	2	3	4	5		
CRUSTACEANS	<1	84.6	30	46.2	67	50.9	3.8	98.5	100	75	63	100		
euphausiids	<1	84.5			67	40.4	1.1	98.4	100			100		
amphipods	<1	0.1			<1	4.3	2.7	0.1	<1			5		
shrimps			24									69		
FISH	81.6	15.4	70	53.2	33	48.6	95.2	1.5	40	72	59	74		
CEPHALOPODS	18.6			0.6	<1	+	1.0			13	47			

Non-breeding: (1) Macquarie I. (Hindell 1989). Feeding young: (2) King George I. (Volkman *et al.* 1980). (3) Marion I. (LaCock *et al.* 1984). (4) Marion I. (Adams & Wilson 1987). (5) S. Georgia (Croxall & Prince 1980). (6) S. Shetland Is (Jablonski 1985).

13.8; 6), those containing *N. squamifrons*, 13.6 km (2.2–103; 5).

At **Bird I., S. Georgia** (43 stomachs, adults feeding chicks 51–72 d old; Croxall & Prince 1980) crustaceans euphausiids *Euphausia superba* 4.0–6.5 cm, 66% wt., 88% no. crustaceans, 100% freq., 5.40 cm (0.33; 54), 1.5–2.5 cm: <1, 6, 5; *E. frigida*: 1, 6, 7, amphipods *Themisto gaudichaudii*: <1% no.; fish Nototheniidae 10–25 cm incl. *Notothenia rossii*, *Nototheniops larseni*, Channichthyidae 20–35 cm incl. *Champocephalus gunnari*. Proportion of fish increased in later samples as that of euphausiids declined. In subsequent study at **S. Georgia** (Croxall *et al.* 1988) individuals ate either predominantly *E. superba* 91% wt., 5.0 cm (2.8–6.4; 3900) with a few fish or predominantly *Notothenia rossii*, *N. neglecta* 130 g (27–1170), 14–42 cm, *Champocephalus gunnari* 22 g (16–34), 16–20 cm, usually one species in any one stomach.

Other records: at Ardley I. took *Pleurogramma antarcticum* in spring but in summer only *Euphausia superba* 3.47–4.50 cm (1220 euphausiid per stomach, 36 samples; Valencia *et al.* 1988); at Iles Kerguelen, Nototheniidae (Falla 1937) and other unidentified fish (Loranchet in Murphy), as also at Falkland Is (Bennett in Murphy); at Heard I. (11 stomachs; Ealey 1954) mostly fish (*Notothenia coriiceps*, *N. cyanobranca*; 700 g in one bird), some cephalopods and crustaceans amphipods *Hyperia galba*, *H. spinigera*, *Themisto antarctica*; one bird caught in net at 100 m depth contained eight fish *Notothenia gibberifrons* (9.0–12.0 cm), four other stomachs also containing *N. gibberifrons* as well as euphausiids and cephalopods (Conroy & Twelves 1972); food of six birds breeding Antarctic Pen. largely euphausiids (960 in one stomach), some fish (Bagshawe 1938); four collected Signy I. held mostly small fish with a few amphipods (White & Conroy 1975).

INTAKE Size of meal for 30-day-old chicks at Marion I. 147 g (64; 7–498; 64; LaCock *et al.* 1984), for 51–72-day-old chicks at S. Georgia 887 g (223; 43; Croxall & Prince 1980). At King George I. contents of chicks' stomachs increase from 392 g to 635 g by 42 days old (adult stomach contents = 0.058 chick mass + 0.382, $r=0.53$, $n=36$; Trivelpiece *et al.* 1987); contents of adults' stomachs at same site Nov.–Feb. 805 g (210; 915; 1985). Mean daily growth rate S. Georgia 85 g (Croxall 1984), Crozet Is 87 g (Despin 1977) and about 75 g (Despin 1972). Each chick at King George I. fed 1.92 times/day during guard-stage, feeding interval 12.5 h (SE 0.4; Trivelpiece *et al.* 1987). Fish digested after fasting at 11%/h (Jablonski 1985).

SOCIAL ORGANIZATION Probably gregarious at sea. At Heard I., hundreds of birds seen porpoising together more than a kilometre from shore (Downes *et al.* 1959). Come ashore about sunset and depart before dawn (van Zinderen Bakker 1971a).

BONDS Adults breed from 3 years of age (Croxall & Prince 1983), but at S. Shetlands both males and females breed at 2 years old (W.Z. Trivelpiece). Both parents incubate and tend young until fledging. Up to 90% of surviving pairs reunite next season, though nest-sites change often (W.Z. Trivelpiece).

BREEDING DISPERSION Colonial. At Macquarie I., colonies of 2–271 pairs (Robertson 1986); at Heard I., colonies ranged from 40–1055 pairs (K. Green); on Antarctic Pen., 12 000 birds on three islands off Danco Coast (Bagshawe 1938). Nests usually more than one metre apart; allows birds to move through colony without causing disturbance (van

Zinderen Bakker 1971a); level of disturbance at periphery of colony probably similar to that at centre (Robertson 1986). Colonies more open and nests more widely spaced than colonies of Rockhopper and Royal Penguins (Downes *et al.* 1959). Sites of colonies may shift from year to year; possibly as defence against parasites (Stonehouse 1967); large infestations of ticks noted in some years at King George I. (W.Z. Trivelpiece), but no parasites found on Macquarie I. (P. Reilly). Sometimes associated with Chinstrap *P. antarctica* and Adelie Penguins, which also infested by ticks. Nest material often stolen from neighbouring nests (Downes *et al.* 1959; van Zinderen Bakker 1971b).

ROOSTING On beaches, and occasionally nesting sites, throughout year. Not known when at sea.

SOCIAL BEHAVIOUR Visual and vocal displays at breeding grounds conspicuous. Little information on integrated flock behaviour.

AGONISTIC BEHAVIOUR After selection of nest-site, males settle first and defend site with ritualized threat postures and calls (van Zinderen Bakker 1971b).

THREAT DISPLAYS. Low-intensity Threat Posture. Raise body and point bill upwards; head turned from side to side observing danger; birds then face danger and hiss. Most often seen in incubating birds. If this fails, high-intensity threat used. **High-intensity Threat Posture.** Stretch neck in direction of intruder while opening and closing bill and occasionally uttering *arr*. May direct peck at intruder, generally missing target. **Aggressive Physical Contact.** Birds stretch towards each other, open bills wide and each turns head c. 20° to the right; then vibrate heads and bills and try to peck one another; accompanied by drawn-out *aaaa*. Behaviour may be repeated two or three times. May occur when birds come too close to occupied nest or if chicks become mixed in pre-crèche stage (van Zinderen Bakker 1971b). **FIGHTING.** Fights between conspecifics common (Stonehouse 1985), but may avoid aggressive interactions with other species. Move from usual landing beaches when these occupied by other species; charge predators such as skuas, giant-petrels and cats (van Zinderen Bakker 1971b).

SEXUAL BEHAVIOUR Males **ADVERTISE** using Ecstatic Display; recognition consists of Mutual (Ecstatic) Displays and Bowing. **Ecstatic Display.** Raises head and body vertically with bill pointing upwards; tail held above ground and flippers held down, near body, never raised; at low intensity, remain silent (van Zinderen Bakker 1971b); at high intensity, emit loud crowing calls (Bagshawe 1938), first being loudest, becoming progressively quieter (see Voice); maintain posture after calling, before relaxing. Performed by solitary males at nest when approached by another bird. After pair-formation, Ecstatic Display performed as **Mutual Display** (Jouventin 1982), which is high-intensity Ecstatic Display performed by both members of pair at site (though calls may differ, see Voice); more frequent once laying over (van Zinderen Bakker 1971b); probably serves to strengthen pair-bond (Bagshawe 1938). Differs from Mutual Display (epigamic) of Adelie and Chinstrap Penguins by absence of head-swaying (Bagshawe 1938; Roberts 1940). Birds may Bow to each other after Ecstatic Display (Bagshawe 1938). **Bowing.** Bird may stand or sit in nest, while other, standing next to it, bends down towards nest, opens bill, displaying bright-red lining of mouth and hisses or wheezes; sometimes cross bills. Likened to movements of bird bringing nesting material to nest and placing it on rim (van Zinderen Bakker 1971b). May be per-

formed 10–20 times in quick succession. Usually performed during change-over at nest; also when mate brings nesting material to nest, Bowing before departing without other bird making any response other than arranging material. ALLO-PREENING not observed. Courtship and copulation take place at nest site; descriptions vary. COURTSHIP. Male seen bringing material to nest-site, standing next to nest before suddenly mounting female from one side (van Zinderen Bakker 1971b). Bagshawe (1938) and Downes *et al.* (1959) recorded Bowing before copulation: birds face each other and both Bow; male slowly moves round behind female and starts Bowing sideways; if female moves forward, display stops. COPULATION. Female, leaning forward or lying down, lifts head and points bill upwards before male mounts (Downes *et al.* 1959) or after (van Zinderen Bakker 1971b). Male mounts female from side, bends forward, points bill and flippers vertically down; after gaining balance, male vibrates flippers against female's neck, then moves backwards, patting female with flippers; birds rub bills. Female lifts tail while male moves back to her rump placing tail beneath female's and making cloacal contact. Only one contact made during each mounting (van Zinderen Bakker 1971b). Other postures (van Zinderen Bakker 1971b): Body-shake, Head-shaking, Both-wing-stretch, Jaw-stretch and Body-stretch. **Body-shake.** Begins with erection of body-feathers, stretching neck and holding flippers horizontally. Shake head, flippers and body from side-to-side; often followed by shaking of tail. Observed in birds that have come ashore or that have risen during incubation. **Head-shaking.** After coming ashore and during feeding in 95% of adults and chicks more than 5 weeks old. **Both-wing-stretch.** Body held upright while head and neck almost parallel to ground; flippers raised behind back, occasionally touching at tips. Occurs in incubating and resting birds. **Jaw-stretch.** Bill pointed upwards, wide open, then closed; seen in incubating birds standing at nest; bird resumes incubation. **Body-stretch.** Combination of Jaw-stretch and Both-wing-stretch. Stand with flippers raised behind back, pointing bill upwards and wide open; stretch neck briefly before lowering head as far as possible, closing bill and returning flippers to side.

RELATIONS WITHIN FAMILY GROUP Males begin building on arrival. Female takes over building after pair-formation while male brings materials. Both parents incubate eggs, with either taking first shift. Female usually goes to sea between laying of eggs, leaving male alone for 1–3 days (W.Z. Trivelpiece). Each shift usually 24 h, but may last up to 4 days (Murphy; Williams & Siegfried 1980). Females' shifts average 4–5 days (1–8), fasting and losing c. 85 g/day (W.Z. Trivelpiece). Nest may be deserted if partner does not return from feeding trip (Trivelpiece *et al.* 1983). Both parents feed chicks until fledging, with continuous brooding for first 3 weeks. Feeding by incomplete regurgitation with chick taking food from adult's gullet. Larger chicks usually fed first in feeding chases (van Zinderen Bakker 1971b).

VOICE Reasonably well known; vocalizations reviewed by Jouventin (1982) and described by van Zinderen Bakker (1971b) and Bagshawe (1938). Noisy during breeding season at colonies and also call at sea round colonies; no information on calling outside breeding season. Utter varying loud crowing or trumpeting calls and grunts and quiet hisses; most calling associated with agonistic and sexual behaviours. At Marion I., during breeding season, part of population ashore all day with influx at sunset; most nest-reliefs occur at about 09:00 and calling associated with this increases at this time; few birds

ashore during day in non-breeding season. Singing highly infectious in colonies. Variation in calls between individuals greater than variation in calls of individuals (Jouventin 1982); adults appear to recognize mate and chick by sight and voice and chicks appear to recognize parents by voice (van Zinderen Bakker 1971b). No information on sexual differences. Apparent geographical variation (not corresponding to sub-specific ranges; Jouventin 1982); two distinct groupings of calls: recordings from Macquarie I and Iles Kerguelen and Crozets similar with slow rhythm, low pitch and long phrases; recordings from S. Orkney Is, S. Georgia and Falkland Is have rapid rhythm, high pitch and short phrases. At Iles Crozet, number of syllables per phrase 24 (14–32; 14), main frequency 1535 Hz (1000–2500; 14), maximum frequency 4410 Hz (2750–6750; 14); corresponding values at S. Georgia were 12 (10–17; 14), 1285 Hz (100–1500; 14), 6535 Hz (5000–7500; 14). **NON-VOCALSOUNDS:** varying claps and pattering sounds made by flippers.

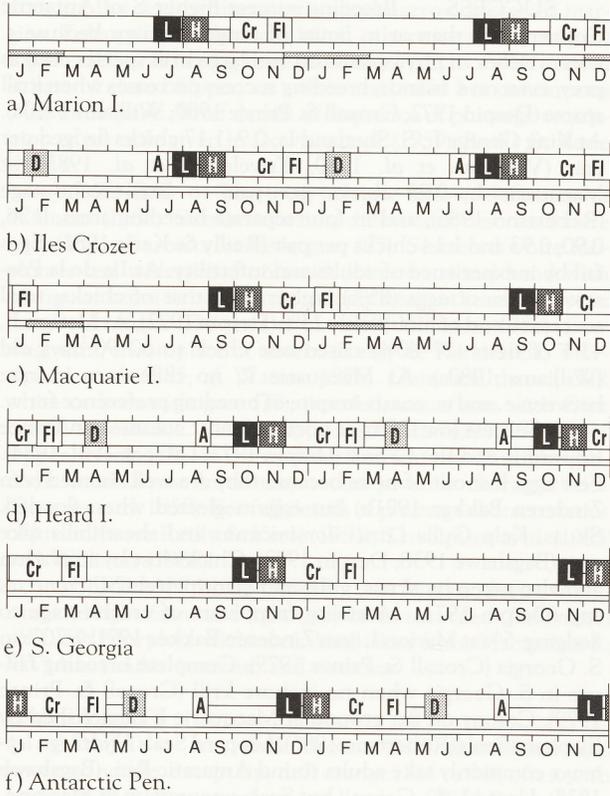
ADULT Ecstatic Call. Loud crowing, braying or trumpeting call given with head and neck stretched vertically, sound produced during exhalation and inhalation; calls are series of 4–5 repeated phrases rendered as *ah, aha, aha, aha, e* (Bagshawe 1938); phrases consist of short noisy inhalatory syllable then a series of highly regular, almost identical, syllables. Birds relax before displaying and calling again. Call given during high-intensity displays; low-intensity Ecstatic Display performed silently; preformed throughout breeding season, and associated with mate-attraction, pair-formation, and re-inforcement of pair-bond; also given during nest-relief with Bowing Display. **Mutual Display Call.** Like Ecstatic Call but possibly more regular with shorter phrases. **Bowing Call.** Very soft, almost inaudible, hissing, often not heard in noise of colony; always associated with Bowing Display. Most common display; can be repeated up to 20 times. **Threat Calls.** In Low-intensity Threat, birds hiss (as in Bowing); in High-intensity Threat, utter grunting *arrrrr*. **Tête-a-tête.** Give drawn-out *aaaaa*; display and call usually repeated 2–3 times. **Contact Call.** Reported by Jouventin (1982) but not described; brief low-pitched clipped call, like abbreviated version of display calls.

YOUNG Small chicks beg with *cheeping* sounds. Utter modulated whistle that is constant within individuals but differs between individuals. Adult calls develop when moulting.

BREEDING Partial studies from several subantarctic islands; studied at Marion I. by Williams (1980a); information contributed by K. Green. Colonial, in small (<100 pairs) to large (thousands of pairs) congregations; sites may be changed short distances (100–200 m) (Despin 1972) from year to year. May be mixed with Adelie Penguins on S. Shetland Is (Yeates 1975) and Chinstrap Penguins on Antarctic Pen. (Bagshawe 1938; Yeates 1975).

SEASON Laying starts later with increasing latitude: Marion I., first week June (Crawford 1952), 16 June (van Zinderen Bakker 1971b), first laying 24 June (Williams 1980a); Prince Edward I. and Iles Crozet, 29 June (Despin 1972), July–Aug. (Falla 1937; LaCock *et al.* 1984); Iles Kerguelen, 29 Aug. (Paulian 1953); Macquarie I., 12 Sept. (Tulloch 1916), 9 Sept. (Gwynn 1953); Heard I. (farther N but S of Antarctic Convergence), 26 Oct. (Gwynn 1953), 15 Oct. (Downes *et al.* 1959); S. Georgia, 21 Oct. (Roberts 1940), late Oct. (Davis *et al.* 1983); S. Orkney Is, 6 Nov. (Clarke 1915); Antarctic Pen., 18 Nov. (Gain 1914), 29 Nov. (Bagshawe 1938). Probably varies

according to snow-cover (Downes *et al.* 1959). Most clutches laid during July but laying recorded till end Nov. on Ile de la Possession (Despin 1972). Hatching at Elephant I., S. Shetland Is, from 18 Nov. to 16 Jan. with peak late Nov.-early Dec. (Furse 1979).



SITE Elevated sites overlooking sea, away from interference by Elephant Seals *Mirounga leonina* and floods; on ridges on Signy I. (White & Conroy 1975; Stonehouse 1985); on high ground with access to beaches by gullies on Heard I. (Downes *et al.* 1959); in valleys with direct access to sea on Ile de la Possession, Iles Crozet (Despin 1972). Most colonies at periphery of islands, usually behind immediate coastal edge (Rand 1955; Downes *et al.* 1959; Despin 1972). At King George I., mean distance of colonies from sea, 92 m (Volkman & Trivelpiece 1981); at Heard I., colonies farther inland in years when snow persists along coast (Downes *et al.* 1959). At King George I., 66.5% birds nested at 1-10 m asl; 22.6% at 11-20 m asl; 10.9% at 21-30 m asl; and none at 31-40 m asl (Volkman & Trivelpiece 1981), indicating preference for low altitude when nesting with other pygoscelid penguins. Colonies at 60 m asl on Iles Crozet (Falla 1937) and up to 70 m above high-tide level on Macquarie I. (Reilly & Kerle 1981). Colonies at Danco I., Port Lockroy and Neko Harbour appear to have been settled from lower levels upward, as numbers of nests and density decrease with elevation (Muller-Schwarze & Muller-Schwarze 1975). But on S. Georgia, nest at 200 m asl and 2 km from shore; wherever high land accessible it is used, even if unoccupied suitable habitat near sea (Murphy). Most nesting areas flat or gently sloping; at King George I., mean slope of colony sites 4.0° (Volkman & Trivelpiece 1981). At Iles Crozet, mean wind-speed of 4.6 m/s measured at colony

on slope; lower than in other parts of island (Despin 1972). Vegetation at some colony sites is absent or sparse where Elephant Seals have moulted (Despin 1972; Downes *et al.* 1959); or nests may be built among tussock grass *Poa* spp, *Acaena insularis*, *Azorella* hummocks or *Cotula* sp. (Falla 1937; Rand 1955; Downes *et al.* 1959; Despin 1972; Robertson 1986). Individual nests often on *Azorella* hummocks or tussocks of *Poa cookii* on Heard I. (Downes *et al.* 1959): on tussocks of *P. foliosa* on Macquarie I. (Gwynn 1953).

NEST, MATERIALS Scraped-out hollow, in which nest built of grass, stones, tail-feathers, shells, bones, moss, *Azorella* (Bagshawe 1938; Stonehouse 1985), to form mound 10-20 cm high, 45 cm across (Bagshawe 1938; Yeates 1975). One nest made of 1700 stones, 70 tail-feathers of Gentoo Penguins (Bagshawe 1938). Nests of stones characteristic on Antarctic Pen. (Bagshawe 1938) but unusual on Heard I., where nests on peaty soil (Downes *et al.* 1959). Males start building nests crudely and use site for displaying; after pair-formation female takes over building and male brings material (van Zinderen Bakker 1971b; Despin 1972) though Roberts (1940) claimed that either sex started building. Least distance between nests c. 1 m (K. Green). On Ile de la Possession, because area of colonies may shift slightly from year to year, old nest-sites are not re-used (Despin 1972).

EGGS Rounded or subspherical; not glossy, with white chalky coating; greenish-white with blue-green inner shell showing through coating (Murphy).

MEASUREMENTS, WEIGHTS. At Heard I., A-egg (first) usually slightly larger than B-egg (second); however, at Marion I. no differences in size between A- and B-eggs in replacement clutches (Williams 1980a).

Table 2.

Location	Length	Width	Ref
Marion I.	68.1 (1.3; 61.7-74.4; 80)	57.7 (1.9; 52.6-62.5)	1
Ile de la Possession	68.6 (65-73.2; 26)	58.9 (56-62.6)	2
Heard I.			
A-egg	71 (2.5; 66-76; 13)	59 (1.8; 57-62)	
B-egg	69 (2.5; 64-74; 13)	58 (1.8; 56-61)	3
Macquarie I.	67 (63-71; 68)	56 (53-60)	4
	WEIGHT:		
Marion I.			
A-egg	142 (12; 117-158; 13)		1
B-egg	134 (113-157; 13)		1
Ile de la Possession	139 (125-160; 26)		2

References: (1) Williams (1980a); (2) Despin (1972); (3) Gwynn (1953); (4) Falla (1937).

CLUTCH-SIZE Two. On Antarctic Pen., C/3 recorded in 14 nests and C/4 in one nest in colony of 6000+ pairs (Bagshawe 1938); at Marion I., no records of more than C/2 (Williams 1980a). On Ile de la Possession one C/3 noted in four much-visited colonies (Despin 1972). Replacement after loss reported, 66 days later (Despin 1972; Williams 1980a).

LAYING At intervals of about 72 h (Gwynn 1953); 3-5 days (once of 95 h) (Despin 1972). Time of day of laying not known.

INCUBATION By both sexes, fully prone (Wil-

liams 1980a); starting seriously with B-egg. Either parent takes first stint (Stonehouse 1985). Change-over about once every 24 h (Trivelpiece *et al.* 1983) but may vary from 1 to 4 days (Murphy; Williams & Siegfried 1980). Despin (1972) stated that incubation lasted for 11–12 shifts in all, that male took the greater share, shifts averaging 3.3 days, and female less with shifts averaging 2.8 days. **INCUBATION PERIOD:** 35–36 days (Bagshawe 1938; Gwynn 1953) from laying of B-egg. Despin (1972) had 34 days (33–35). Hatching generally 24–48 h apart, but sometimes at same time (Despin 1972). First chick to hatch conspicuously larger than second (van Zinderen Bakker 1971b). On n. breeding areas, smaller chick of pair usually dies of starvation but, if food plentiful, both can be reared (Croxall & Prince 1983; van Zinderen Bakker 1971b); hardly 1% of 300 pairs at Ile de la Possession raised two chicks (Despin 1972); none known to do so at Marion I. (Williams 1980a). On Antarctic Pen., both chicks fledge and nests with 2 chicks more common than those with 1; i.e. failure is all or nothing (W.Z. Trivelpiece). Daily feeding during courtship and incubation maintains condition of parents and may lessen risk of desertion, as happens more often with Adelie and Chinstrap Penguins (Trivelpiece *et al.* 1983).

YOUNG Semi-altricial, nidicolous. Hatched with long, fairly thin protoptile, dark brown above, white below, which replaced in first 10 days by light-coloured mesoptile, shorter and much thicker; small black rectrices appear when about 22 days old (Despin 1972; Williams 1980a). Both parents brood and guard chicks; for first three weeks, stints of brooding exceed 24 h (Williams & Siegfried 1980). Chicks begin to emerge from under parent when 7–10 days old and then sit in front of it, sheltering under it again at least alarm. Chicks begin to make short excursions away from nest at c. 20 days old, often returning (Despin 1972); guard-stage lasts for 25 days (3.9; 20–33; 10) (Williams 1980a). Small crèches form gradually until all are in crèches about one month later, individuals generally becoming fully crèched c. 29 days old. Crèche breaks up daily in the evening, when adults return at 17:00–20:00 (Despin 1972). Both parents feed chicks by incomplete regurgitation, chick taking food from adult's throat. Larger chick usually fed first when chicks are mobile in crèche stage (van Zinderen Bakker 1971b). At first, adults feed chicks on nest and chicks may return to nest to be fed for 9 days after joining crèches, even at night; often seen begging vigorously from adults at nest and also making feeding chases, which may take them far from colony (>300 m) (Despin 1972). **PERIOD TO FLEDGING:** about 100 d (Volkman & Trivelpiece 1980); about 90 days (Bagshawe 1938); 74 days (Volkman *et al.* 1980); 80–90 days (Despin 1972). At Marion I., period longer than elsewhere (LaCock *et al.* 1984). Rearing of chicks almost twice as long as that in Adelie and Chinstrap Penguins (Croxall & Prince 1983; Volkman & Trivelpiece 1980).

GROWTH Mean weight at hatching, 94 g (8.9; 77–113; 24), A-chicks being significantly heavier than B-chicks (Williams 1980a). At first, growth slow for about 3 weeks; then increases rapidly between 28 and 40 days old and decreases afterwards till departure. First period corresponds to time when adults have two chicks to feed. Increased rate of growth starts with death of one chick in n. breeding populations or when chicks join crèches and allow both parents to forage simultaneously (W.Z. Trivelpiece). Final period of decreasing rate of growth corresponds to crèching and moult, but chicks fed throughout and even after moult and after having been to sea (Despin 1972). However, Williams (1980a) recorded linear increase in weight till c. 70 days and then decrease to c. 4 kg

until independence.

FLEDGING TO MATURITY After moulting, chicks begin to go to sea but spend more time on beaches than in water and may return to colonies in evening to be fed. Survival of immatures not known. Survival of adults about 80% (Croxall & Prince 1983).

SUCCESS Breeding success higher S of Antarctic Convergence than at n. limits of range, perhaps because s. waters richer in phytoplankton and large krill species used as prey; even on s. islands, breeding success decreases when krill sparse (Despin 1972; Croxall & Prince 1980; Williams 1980a). At King George I., S. Shetland Is, 0.9–1.17 chicks fledged per pair (Volkman *et al.* 1980; Trivelpiece *et al.* 1983); at Macquarie I., 0.98 chicks per pair to late crèche-stage (Robertson 1986), and in four separate breeding areas, 0.36, 0.90, 0.93 and 1.14 chicks per pair (Reilly & Kerle 1981). Eggs fail by inexperience of adults and infertility. At Ile de la Possession loss of eggs (85%) higher than that of chicks; total success to end of moult only 25% (Despin 1972). At Marion I., 43% of nests (17–60%) raised one chick to 60–90 days old (Williams 1980a). At Macquarie I., no difference in rate between e. and w. coasts in spite of breeding preference for w. coast. Success low (25%) at northernmost colonies on Prince Edward Is and Iles Crozet (Despin 1972; LaCock *et al.* 1984). Few eggs lost out of nests because they are well rimmed (van Zinderen Bakker 1971b) but eggs neglected when flooded. Skuas, Kelp Gulls *Larus dominicanus* and sheathbills take eggs (Bagshawe 1938; Despin 1972). Chicks lost by starvation and also taken by skuas, gulls and giant-petrels *Macronectes* spp (Despin 1972). Mortality from start of crèche-stage to fledging: 5% at Marion I. (van Zinderen Bakker 1971b); 20% in S. Georgia (Croxall & Prince 1979). Complete breeding failure in S. Georgia when no inshore krill (Croxall & Prince 1979). Colony on flat ground at Macquarie I. demolished by Elephant Seals (Robertson 1986). Leopard Seals *Hydrurga leptonyx* commonly take adults round Antarctic Pen. (Bagshawe 1938), Heard I. (K. Green); but Seals uncommon at Marion I. (van Zinderen Bakker 1971b). Skuas, Kelp Gulls and feral cats also take young.

PLUMAGES Nominate *papua*.

ADULT HEAD AND NECK. Entirely dark black-brown (119) to base of neck. Above each eye, broad white triangular patch of feathers, joined by narrow coronal band of white feathers across hindcrown, continuous with narrow white eye-ring. Scattered short white filoplumes, profuse on hindcrown, auricular area and nape; fewer at lores and lower neck. **UPPERPARTS.** In fresh plumage, feathers on mantle, back and rump, short and dense, dark black-brown (119); tips, light blue-grey (88). In worn plumage, before moult, feathers of dorsum, dull and dark brown (119A). A few short white filoplumes scattered on outer mantle. Rachis on dorsum, laterally flattened, black (89). Some lowermost upper tail-coverts white, or tipped white (Falla 1937). **TAIL.** Rectrices, long, rigid at base, dark black-brown (119); tips, light blue-grey (88), prone to wear; outermost pair vary, entirely white, or edged white (Falla 1937; Rand 1954). **FLIPPER.** Feathers scale-like anteriorly, longer posteriorly, ordered in distinct rows. Dorsal surface, dark black-brown (119); tips, light blue-grey (88), more prominent posteriorly and near tip of flipper. Two posterior rows of feathers on flipper, white, c. 7 mm wide; narrow white anterior margin extends from tip to base. **UNDERPARTS.** Entirely white from base of neck; slight inward progression of white feathers extending upwards near axilla, as straight line

to side of thighs. Dorsal surface of thighs, similar to back. FLIPPER. White, except for small black-brown (119) patch at tip.

DOWNY YOUNG In protoptile, entire dorsum, dark brown (121). Entire underparts, from interramal space, white. Tail tuft, as dorsum. Dorsal surface of flipper, similar to dorsum, but with white anterior and narrow posterior margins. Teleoptile, thicker and hairy, otherwise similar to protoptile; differs in having large prominent patch of white down at base of closed flipper, its extent concealed but continuous with underparts. Brief details of sequence of plumage acquisition to juvenile given in Downes *et al.* (1959), Reilly & Kerle (1981).

JUVENILE The term juvenile follows definition of Williams (1988). Similar to adult, differences described here only. Tips of crown feathers, grey (87). Scattered white filoplumes less widespread on head. Join of coronal band with triangular supra-orbital patch, incomplete, not reaching eye in most individuals (Downes *et al.* 1959; Williams 1988). Eye-ring, thin, incomplete or absent (Reilly & Kerle 1981; Trivelpiece *et al.* 1985; *cf.* Watson 1975). Chin and throat, dull white or brownish grey (79), mottled, sometimes with faint barred appearance. Thighs, tipped dark blue-grey (78). Tip of flipper, black (89) on ventral surface for one-third length. Some second-year birds may retain juvenile characteristics (Downes *et al.* 1959). For full details of plumage characteristics of juveniles see Reilly & Kerle (1981), Trivelpiece *et al.* (1985) and Williams (1988).

ABERRANT PLUMAGES Albinism, partial albinism, and light-fawn and light-grey birds recorded (Downes *et al.* 1959; Murphy). Melanistic bird (skin from Macquarie I.; MV) has similar ventrum and dorsum.

BARE PARTS

ADULT Iris, dark brown (219). Latericorn and lower mandible, except tip, dull orange (116 to 94), often with orange-buff (118) tone (photos in Lindsey 1986). Recorded as orange to salmon-pink (Reilly & Kerle 1981). Tip of culmen and of lower mandible, black-brown (119). Strip of orange on culmen, possible indicating sexual maturity, mean depths of bill greater in sample measured by Reilly & Kerle 1981. Further study of this character needed. No sexual dimorphism in colour of bill (Reilly & Kerle 1981) but noted by Despin (1972). Legs and feet, salmon (106), or paler with orange-buff (118) tone (photos in Lindsey 1986). Soles, black-brown (119). Varying colours of bill and feet noted (Falla 1937; Downes *et al.* 1959). Suggestion that Heard I. birds duller in colours of feet and bill (Falla 1937), not confirmed by examination of photographs (R. O'Brien).

DOWNY YOUNG In protoptile, iris, dark blue initially; after a week, dark blue-brown; finally dark brown (Downes *et al.* 1959). Bill similar to feet, which pale salmon. Egg-tooth, white (Falla 1937). In teleoptile, iris, brown (-). Bill, similar to adult and juvenile, but most of latericorn and lower mandible, buff (118); noted as yellow by Rand (1954). Legs and feet, buff (124) (photo in Lindsey 1986).

JUVENILE Similar to adult, except latericorn and lower mandible, more orange buff (118).

MOULTS

ADULT POST-BREEDING Complete. At Macquarie I., begins Jan., most in Mar.; not synchronic in majority, duration extended (Downes *et al.* 1959). At Macquarie I., duration 15–21 days (Reilly & Kerle 1981). For

full details of sequence see Reilly & Kerle (1981). Temporary partial retention, 'partial moult' of adult body feathers observed; possibly increasing insulation for duration of short swim (Reilly & Kerle 1981). Post-breeding birds distinguished from post-juvenile by absence of tail; rectrices last to grow (Reilly & Kerle 1981). At Marion I., moult Dec.–Mar. (Rand 1954; van Zinderen Bakker 1971b). First new feathers appear on back; spread to front, flippers and tail; last feathers to moult on head and neck (van Zinderen Bakker 1971b). Progression of moult requires study based on development of feathers; use details in Brown (1986) and Groscolas (1976) as guide. More details of moult in Mougín (1972) and Croxall (1982).

JUVENILE Protoptile replaced by teleoptile at end of first week (Reilly & Kerle 1981). First moult starts in ninth week after hatching, begins on head simultaneously with emergence of rectrices; a week later moult complete on head and mantle. Last down shed on belly (Downes *et al.* 1959; *cf.* Reilly & Kerle 1981); last down shed 63–71 days (Reilly & Kerle 1981). For full details of plumage development see Reilly & Kerle (1981).

POST-JUVENILE Moult c. 14 months of age (Williams 1988), in Feb.; most in pre-moult late Jan. (Downes *et al.* 1959; Reilly & Kerle 1981).

MEASUREMENTS Subspecies *papua*. (1) Falkland Is (Stonehouse 1970). (2) Falkland Is (Despin *et al.* 1972). (3) S. Georgia (Stonehouse 1970). (4) S. Georgia (Despin *et al.* 1972). (5) Iles Crozet (Stonehouse 1970). (6) Ile de l'Est, Iles Crozet (Despin *et al.* 1972). (7) Iles Kerguelen (Stonehouse 1970). (8) Iles Kerguelen (Despin *et al.* 1972). (9) Heard I. (Stonehouse 1970). (10) Heard I. (Despin *et al.* 1972). (11) Macquarie I. (Stonehouse 1970). (12) Macquarie I. (Despin *et al.* 1972). (13) Macquarie I., adults, live (Reilly & Kerle 1981). (14) Marion I. (Despin *et al.* 1972).

		UNSEXED
FLIPPER	(1)	225.0 (1.22; 15)
	(2)	225.0 (-; 194–243; 15)
	(3)	217.0 (1.00; 16)
	(4)	217.0 (-; 190–230; 16)
	(5)	240.0 (-; 1)
	(6)	247.0 (-; 230–270; 22)
	(7)	211.0 (1.47; 18)
	(8)	211.0 (-; 188–231; 19)
	(9)	211.0 (-; 2)
	(10)	211.0 (-; 2)
	(11)	215.0 (1.01; 23)
	(12)	215.0 (-; 192–235; 23)
	(13)	230.0 (0.8; 210–240; 19)
	(14)	238.0 (-; 225–248; 2)
TAIL	(13)	143.0 (6.2; 130–153; 12)
BILL	(1)	56.0 (0.45; 15)
	(2)	56.0 (-; 48–65; 15)
	(3)	51.0 (0.50; 16)
	(4)	51.0 (-; 40–61; 16)
	(5)	61.0 (-; 1)
	(6)	60.8 (-; 56–71; 27)
	(7)	53.0 (0.51; 19)
	(8)	53.0 (-; 42–63; 21)
	(9)	52.0 (-; 2)
	(10)	52.0 (-; 3)
	(11)	53.0 (0.28; 23)
	(12)	53.0 (-; 49–59; 23)
	(13)	56.3 (3.3; 48.3–63.8; 136)

	(14)	59.3 (-; 56.3-64; 4)
BILL D	(13)	18.3 (1.6; 15.3-22.2; 156)
BILL W	(13)	10.0 (0.8; 8.6-11.3; 16)
FOOT	(1)	132.0 (0.27; 15)
	(3)	123.0 (0.78; 16)
	(5)	130.0 (-; 2)
	(7)	121.0 (0.90; 19)
	(9)	116.0 (-; 2)
	(11)	121.0 (0.60; 21)

Subspecies *papua*. S. Georgia (Stonehouse 1970).

	MALES	FEMALES
FLIPPER	241.0 (0.52; 32)	231.0 (0.65; 32)
FOOT	133.0 (0.40; 32)	124.0 (0.42; 32)

Subspecies *ellsworthi*. (1) S. Orkney and S. Shetland Is (Stonehouse 1970). (2) S. Orkney and S. Shetland Is (Despin *et al.* 1972). (3) Antarctic Pen. (Stonehouse 1970). (4) Antarctic Pen. (Despin *et al.* 1972).

	UNSEXED
FLIPPER	(1) 197.0 (0.68; 17)
	(2) 197.0 (-; 184-208; 17)
	(3) 205.0 (-; 2)
	(4) 200.0 (-; 187-209; 20)
BILL	(1) 44.0 (0.28; 17)
	(2) 44.0 (-; 40-50; 17)
	(3) 47.0 (-; 2)
	(4) 47.6 (-; 44-53; 20)
FOOT	(1) 112.0 (0.59; 17)
	(3) 112.0 (-; 2)

Murphy gives some measurements, perhaps including *P.p. ellsworthi* (unrecognized at that time). Full details of rates of growth of chicks in Gain (1914); at Marion I., in Williams (1980a); at King George I., S. Shetland Is, in Volkman & Trivelpiece (1980).

WEIGHTS Weights in kg. (1) S. Georgia (Stonehouse 1970). (2) S. Georgia, adults (Croxall & Prince 1980). (3) Macquarie I., adults (Reilly & Kerle 1981).

	MALES	FEMALES
(1)	6.4 (0.70; 32)	5.5 (0.65; 32)

	UNSEXED
(2)	6.82 (0.598; 43)
(3)	5.7 (0.61; 4.2-7.2; 97)

For seasonal variation at S. Georgia, Dec.-Feb., see Croxall & Prince (1980). During moult, at Macquarie I., adults lose 3.3% of body-weight/day (Reilly & Kerle 1981). Weight loss in moulting birds, 210 g/day (unknown sample); initial weight 9800, final 5400; for full details see Croxall (1982). For details of changes in weight of chicks see Bagshawe (1938), Despin (1972, 1977), Reilly & Kerle (1981), Williams (1980a), Volkman & Trivelpiece (1980) and Taylor (1985).

STRUCTURE Flightless. Flipper, hard and bony, long, broad at base. Feathering of body dense, strongly lanceolate; rachis broad and flattened at tip; imparts glossy appearance. Tail, long and rectangular; 14-18 rectrices (Falla 1937), t1 longest, t8 92-97 mm shorter. Ventral surface of rachis on rectrices, strongly concavely ridged. Bill, slender and pointed; less robust in *ellsworthi*. 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 toe. Pads of soles thick. Claws, long, thick and curved. Middle toe longest; outer toe 89%, inner 62%, hind 18%.

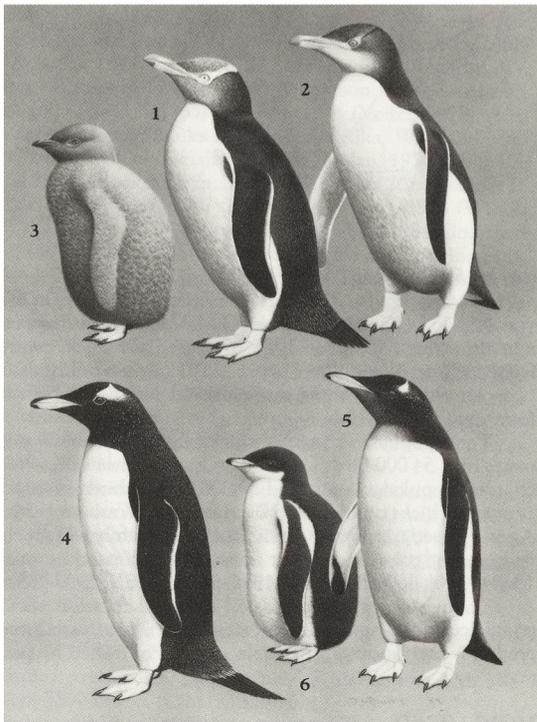
GEOGRAPHICAL VARIATION Nominate *papua* differs from *ellsworthi* in larger size and proportions of bill (Murphy 1947; Stonehouse 1970; see Measurements); anomaly with Bergmann's Rule, perhaps due to dietary differences (Williams 1980b). Difference in size between populations on Iles Crozet and Kerguelen possibly due to colder surface oceanic waters (Viot 1987).

RMO

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Volume 1 (Part A), Plate 9

Yellow-eyed Penguin *Megadyptes antipodes*

1. Adult, feet flushed
2. Juvenile
3. Downy young, mesoptile

Gentoo Penguin *Pygoscelis papua*

4. Adult, subspecies *papua*
5. Juvenile, subspecies *papua*
6. Downy young, mesoptile

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