

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 patagonicus King Penguin

COLOUR PLATE FACING PAGE 144

Aptenodytes patagonicas Miller, 1778, *Icon. Anim.* pt 4, Pl. 23; no locality — South Georgia *apud* Mathews.

Named specifically after the region of Patagonia.

MONOTYPIC

FIELD IDENTIFICATION Length 85–95 cm; flipper 320–340 mm; bill 69–78 mm; weight 13.4 kg. Tall stately penguin with striking orange and black head-markings in adult. Long slender decurved bill, black with conspicuous orange or pink mandibular plate. Second largest penguin; smaller, much lighter and more brightly coloured than more southerly congener, Emperor Penguin *A. forsteri*. Sexes similar but females slightly smaller. No seasonal changes. Immatures similar to adults but duller.

DESCRIPTION **ADULT.** Head, chin and throat, black with greenish gloss and bright golden-orange auricular patch (c. 2 cm wide) extending as thin narrowing stripe round sides of neck to upper breast. Dorsal surface from nape to tail and including flippers, silvery grey-blue. Tail, black. Upper breast, golden-orange, merging above with blackish throat

and fading downwards to yellow, then white. Rest of underparts, satin-white. Thin black stripe separates orange auricular patch from blue-grey nape; stripe extends round neck to sides of breast then down to flank, separating white underparts from blue-grey dorsum. Black stripe widest (c. 1 cm) just above base of flipper. Underflipper, white with blue-black at base extending as thin band along leading-edge to extensive blue-black area at tip (but some have entirely white underflippers). Bill, long, slender and decurved. Upper mandible, blackish; lower mandible, black at tip but basal two-thirds orange, pink or lilac. Black feathers on chin under mandible not obvious in profile. Iris, brown or raw umber. Feet and legs, dark grey-black, tarsus unfeathered. Before moult (Sept.–Dec. on Iles Crozet) dorsal feathers become brownish. **IMMATURE.** Similar to adult but auricular patches lemon yellow (whitish when

worn), throat greyish white and crown feathers black with grey tips. Bill, black with mandibular plate streaked pink, becoming ivory-white in older immatures.

SIMILAR SPECIES Can be confused only with larger and much heavier Emperor Penguin. All other penguins are much smaller. Differs from Emperor in having longer bill with feathers of chin not extending over mandibular plate; larger broader mandibular plate, typically orange (c.f. narrow pink stripe of Emperor Penguin). Auricular patch smaller, brighter and more clearly defined by black border but black throat merges with orange upper breast (c.f. sharp demarcation of Emperor). From behind, only little yellow shows on neck, whereas in Emperor Penguin, considerable area of white shows on side of neck. Immatures of the two differ in shape of auricular patch although this not brightly coloured. King Penguins breed on islands close to Antarctic Convergence and occasionally straggle further N, whereas Emperor rarely reported away from pack-ice. **At sea**, auricular patch of King clearly defined with rounded margins and much of grey-blue nape also showing; auricular patch of Emperor Penguin large, irregularly shaped and often extends to below water line as well as round sides of nape.

Mostly restricted to high Subantarctic Zone but range of immatures may overlap with that of Emperor. Highly gregarious on breeding grounds. Walk on land, do not hop. At sea, solitary or in small groups; flocks of over 20 birds only occur near colonies. Porpoising, smooth and heavy with less leaping above water and less splashing than in *Eudyptes* penguins. Monosyllabic contact call used at sea; slightly dissonant cooing note. Display song, polysyllabic trumpeting, musical.

HABITAT Marine, pelagic; N of pack-ice; 45–65°S. In Ross Sea in summer, only N of 61°S, on n. edge of Polar Front Zone (overlying 2°C isotherm, where Antarctic and subantarctic surface-waters meet). Southernmost sightings in Feb. correspond with s. movement of Polar Front. All birds seen where salinities near 34‰ and surface-temperature 4.5 °C, or in warmer eddies surrounded by 4.5 °C water (Ainley *et al.* 1984). Forage usually in ice-free waters (Murphy). At Iles Crozet, mainly forage over shelf and slope areas (Stahl *et al.* in press); concentrate near Polar Front, S of islands (Flora 1981; Harris 1982; Enticott 1986; Stahl 1987; J.A. Bartle; H. Weimerskirch). At Marion I., not seen foraging close to shore (Rand 1955). At S. Georgia, feed over banks 30 km from island, but probably also in kelp close to shore (Murphy). In winter, mostly pelagic; only records at sea in subantarctic waters (J.-C. Stahl). Most juveniles pelagic; observed several hundred kilometres from nearest colony (Ainley *et al.* 1984; J.-C. Stahl).

Breed on subantarctic and Antarctic islands, N of n. limit of pack-ice; using beaches, valleys and moraines free of snow and ice and with easy access to sea. Prefer level ground or gentle slopes at low altitude.

Moult ashore away from nesting grounds; at Heard I., at water's edge on coves and beaches, or by inland lakes and depressions, reached along streams or stony ridges. Deepest dives recorded deeper than for any other aquatic bird except Emperor Penguin; most frequently recorded depth range 5–50 m; dives often >100 m deep, rarely >240 m (Kooyman *et al.* 1982).

At Iles Crozet, breeding habitat destroyed by building activities and road construction (Jouventin *et al.* 1984; Clark & Dingwall 1985). Birds since colonized area cleared nearby

(H. Weimerskirch). Formerly killed by feral dogs on Falkland Is (Murphy).

DISTRIBUTION AND POPULATION Pelagic range Subantarctic and low Antarctic Zones of South Atlantic Ocean, s. Indian Ocean and A'asian sector of Southern Ocean. Breed on subantarctic islands between 46–55°S. Stragglers reach South America and South Africa. Accidental to Aust. and NZ.

Pelagic distribution poorly known; apparently not circumpolar; not yet recorded in s. Pacific Ocean between Antipodes Is and South America. Formerly bred Magellanic region, now only stragglers reported there (Humphrey *et al.* 1970; Hauff 1972; Venegas 1978), including Diego Ramirez Is (Venegas 1982). In Scotia Sea, occasional S. Sandwich Is, Feb.–Apr. (Enticott 1986), S. Orkney Is, Nov.–Feb. (Rootes 1988); accidental S. Shetland Is (Furse & Bruce 1975) and Antarctic Pen. Jan.–Feb. (Smith & Tallwin 1979; Parmelee & Parmelee 1987). In S. Atlantic, recorded at Gough I., Feb., June; at Bouvetoya, Dec.–Jan. (Enticott 1986). Two, possibly three records for South Africa, Jan. (Brooke & Sinclair 1978; Cooper 1978; Ross & Cockcroft 1985). Occasionally reaches Antarctic continent: five records at Terre Adèlie, Jan.–Mar. (Thomas & Bretagnolle 1988).

AUST. VIC.: single, sighted, Port Fairy, 27 Feb. 1973 (Hosken *et al.* 1974; Aust. Atlas); L. Tyers, 4 Jan. 1980 (Aust. Atlas); unverified sighting of two, Noble's Rocks Beach (Aust. Atlas). TAS.: single, killed near Maria I., Dec. 1909 (Hall 1910); Bruny I., before 1924 (Lord & Scott 1924); beachcast remains, Hope Beach, South Arm, 21 July 1956 (Sharland 1956); single, sighted near mouth of Derwent R., 2 Feb. 1970 (Wall 1973); single, sighted Safety Cove, Port Arthur, 15 Mar. 1970 (probably same bird as previous record; Wall 1973; Aust. Atlas); single, Surprise Bay, 26 Mar. 1972 (Hosken *et al.* 1974 *contra* Wall 1973, who listed wrong location); singles, sightings at Dover, 2 Feb. 1973 and about 16 km N of Dover, 10 Feb. 1973 (Wall 1973); moulting, Strahan, Apr. 1974 (Tas. Bird Rep. 1974). WA: fertile egg washed ashore, E of Augusta, 10 Jan. 1974 (Lodge 1976); single, exhausted, Busselton, 8 Sept. 1979 (Aust. Atlas).

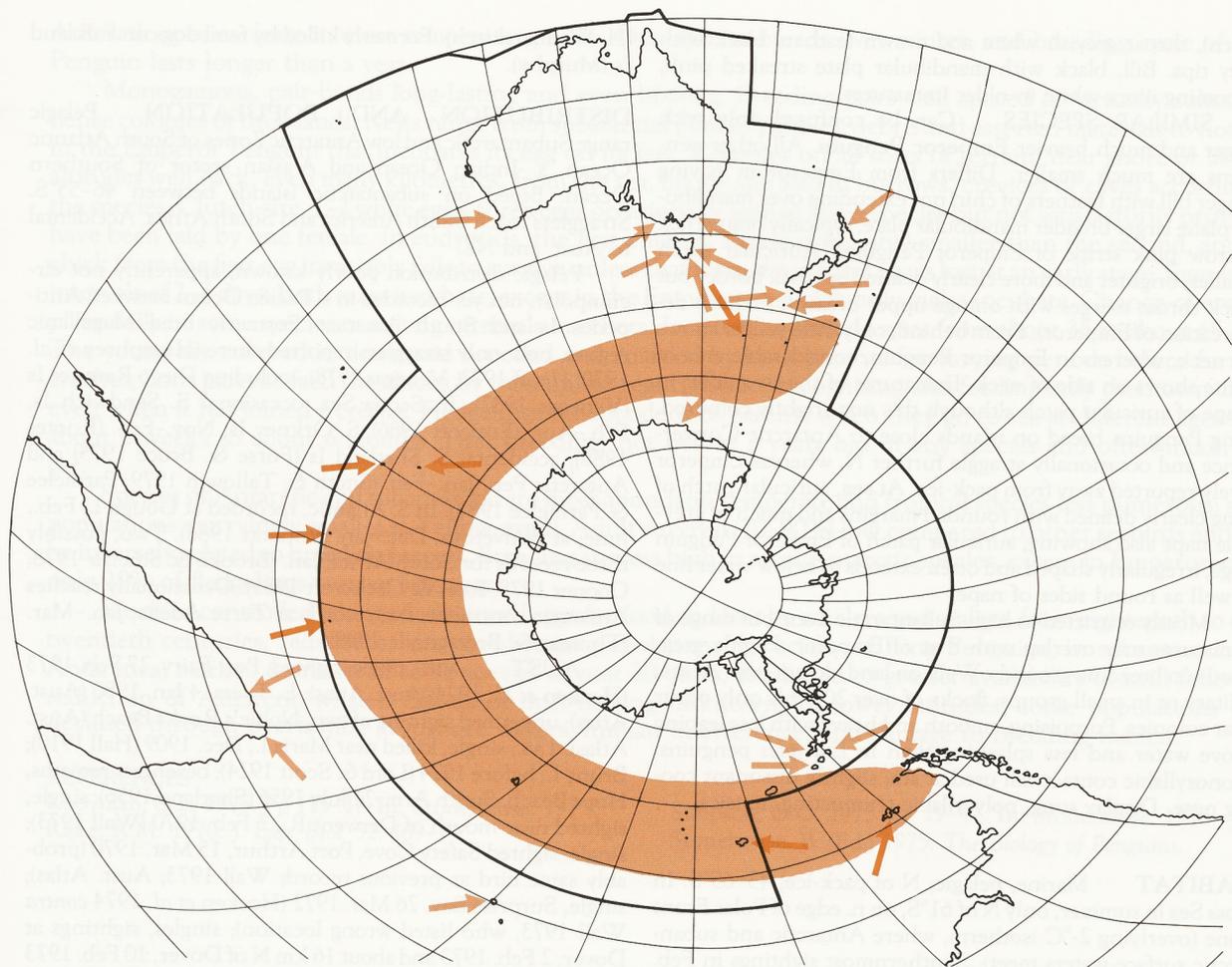
NZ Regular straggler to Campbell I., Aug., Oct., Jan.–Feb. (Bailey & Sorensen 1962; NZCL) but during 1969–79, only one report, Main I., Mar. 1971 (NZ Atlas). Antipodes Is, Feb.–Apr. (Warham & Bell 1979). Also said to have reached Stewart and Snares Is, no further details (Oliver). On mainland, reported from Moeraki (Otago), SI and Auckland Harbour, NI, at some time before 1930 but without further details (Oliver).

BREEDING Localities and estimates of population in Table 1.

Table 1.

| Locality | Year(s) | Population (pairs) | Ref. |
|---|---------|--------------------|------|
| Prince Edward Is | <1979 | 228 000 | 1 |
| Iles Crozet (Possession, l'Est, Cochons) | 1962–70 | 455 000 | 2,3 |
| Iles Kerguelen | 1985–87 | 240 000–280 000 | 4 |
| Heard I. | 1980 | 600 | 5 |
| Macquarie I. | 1980 | 70 000+ | 6 |
| S. Georgia | <1984 | 34 000 | 7 |
| | | c. 100 000 | 8 |

1. Williams *et al.* (1979); 2. Barrat (1976); 3. Despin *et al.* (1972); 4. Weimerskirch *et al.* (1989); 5. Johnstone (1982); 6. Rounsevell & Brothers (1984); 7. Croxall *et al.* (1984a); 8. Croxall *et al.* (in press).



Extraliminally, breed Falkland Is (Croxall *et al.* 1984b; Moreau 1954) and formerly in Magellanic region of South America at Isla de los Estados (Staten Is), where greatly reduced by 1880s (Murphy); no recent indication of breeding (Conroy & White 1973). Breeding at Horn I. (Reynolds 1935) certainly in error.

Status, now stable. Formerly much hunted, several colonies exterminated; possibly whole population on Falkland Is by 1898 (Conroy & White 1973), Heard I. between 1929–48 but with isolated breeding 1949, 1952 (Budd 1975) and in South America. All populations now definitely or probably increasing: annual rate of increase at Iles Kerguelen, 7.3% in three colonies, 1963–85 (Weimerskirch *et al.* 1989); at Macquarie I., 9.7%, 1930–80 (Rounsevell & Copson 1982); at S. Georgia, c. 7.5% between 1936 and 1970–77 (Smith & Tallwin 1979). Higher rate of increase in localities recolonized after abandonment or extermination, which suggests at least partial immigration from elsewhere: Heard I. 15.1%, 1963–80 (Budd & Downes 1965; Johnstone 1982); Falkland Is, c. 14.5%, 1945–83 (Smith & Tallwin 1979; Croxall *et al.* 1984b). Probably also increasing at Marion I. (Williams 1984).

MOVEMENTS Dispersive, possibly partly migratory. Times of arrival and departure from colonies more complex than in other penguins because breeding cycle lasts 14–16

months and birds may not breed annually. At S. Georgia, most successful breeders return for moult and breeding about 2–3 weeks after independence of chick from previous season; most failed breeders and non-breeding adults leave colonies 17 June (26 days; 17 Apr.–30 July; 43), returning 3 Oct. (13 days; 8 Sept.–6 Nov.; 43) but 20% (n=54) occasionally present throughout winter (Stonehouse 1960). Chicks fledge, Nov.–Mar. (Budd 1975; Barrat 1976; Rounsevell & Copson 1982; Croxall & Prince 1987; Weimerskirch 1989). At S. Georgia juveniles absent early–May to mid-Sept. (Stonehouse 1960); at Iles Crozet, immatures absent Mar.–11 Oct. during second year, 2 May–6 Nov. during third year, 26 Apr.–20 Oct. during fourth year (Barrat 1976). Juveniles disperse rapidly in s. Indian Ocean: observed 600 km from nearest colony within 2 months of first fledging (J-C. Stahl) and reported as vagrants S. Sandwich Is (Croxall & Kirkwood 1979), Bouvetoya (Watkins 1981), Antipodes Is (Warham & Bell 1979) and Ross Sea (Ainley *et al.* 1984) and birds of unknown age recorded Terre Adélie, 11 Jan.–8 Mar., mostly in moult (n=5; Peters; Thomas & Bretagnolle 1988) and Signy I., S. Orkney Is, Nov.–Feb. (8; Rootes 1988). At Iles Crozet, may wander and moult away from breeding colony (Barrat 1976) with possible regular movement to Marion I. (see Banding). Also recorded moulting away from natal colony Heard I. (Downes *et al.* 1959) and S. Georgia (Stonehouse 1960).

BREEDING Foraging range from Marion I., 255 km (80–418) when feeding small chicks, 301 km (77–902) feeding

large chicks Oct.-Dec. (Adams 1987); Iles Crozet, max. potential foraging range in spring 1400 km (Ridoux *et al.* 1988); S. Georgia, 424 km when feeding chicks (Croxall & Prince 1987).

BANDING All recoveries from SABRU banded birds. Only one instance of inter-island movement within Iles Crozet (Barrat *et al.* 1973) but 12 birds from Iles Crozet recovered Marion I. (1000-1120 km W) after 22 months (18; 7-69): 10 Oct.-Jan., 1 May, 1 July (Weimerskirch *et al.* 1985; Gartshore *et al.* 1988). Interval between banding and recovery suggests that most are immatures between first appearance of adult plumage (2+ y) and first breeding (4+ y; Gartshore *et al.* 1988) but one banded Iles Crozet 17 Nov. recovered with chick, Marion I. 15 July (Burger & Morant 1977) giving maximum 2.5 months to complete movement in time for breeding. One bird banded Marion I. recovered Iles Crozet Jan. after 22 months (Brown & Oatley 1982). Juveniles and immatures disperse more widely than adults: rate of distant recoveries from Iles Crozet: juveniles 0.67% (n=1803), adults 0.14 (7737; Weimerskirch *et al.* 1985). Widest movements during first year at sea: 16 chicks banded Iles Crozet recovered elsewhere after 18 months (12-82); 13 from Marion I., one from Iles Kerguelen, one from Macquarie I., one from Heard I. (Barre *et al.* 1976; Weimerskirch *et al.* 1985; Gartshore *et al.* 1988; Woehler 1989).

FOOD Mostly small myctophid fish with some small cephalopods in winter at Marion I., Iles Crozet and Macquarie I.; at S. Georgia mostly large cephalopods. **BEHAVIOUR.** Feed underwater by pursuit-diving at speeds of up to 12.1 km/h and frequency of wing-beats 2.85 beats/s, with greater complexity of submarine movements than other penguins (Clark & Bemis 1979). At S. Georgia about 56% dives (n=2595) 5-50 m, 0.1% 240-290 m (electronic recorder), with 10% success if taking cephalopods (Kooyman *et al.* 1982). To meet energetic requirements at S. Georgia only 5% dives need be successful with 21.6 g food being caught per dive (Croxall & Lishman 1987). On foraging trips, average travelling speed 8.7 km/h (1.2; 7.0-10.8; 15) for 19.0% of time (16.5; 8-38; 3) when feeding small chicks, 36.0% of time (5.5; 28-44; 6) when feeding large chicks (Adams 1987). Probably feed night and day with deep dives during day, shallow dives at night (Croxall *et al.* 1988). Has largest span between tips of opened jaws of any penguin measured (Zusi 1975), assumed to allow ingestion of larger food, with rows of spines on tongue and sides and roof of mouth (Murphy).

NON-BREEDING One individual from Drake passage contained cephalopod beaks (Linkowski & Rembieszewski 1978).

BREEDING At Marion I. (120 samples pumped from stomachs, 38522 items, ads. and chicks; Adams & Klages 1987) fish 86.5% wet mass: *Paralepis coregonoides* 0.2% no., 30.0% freq., *Electrona carlsbergi* 13.2, 70.0 (90% 5.1-11.8 g, 7.06-9.8 cm), *Gymnoscopelus* 0.2, 3.3, *Krefflichthys anderssoni*/*Protomyctophum tenisoni* 31.8, 85.0 (modal mass 1.9-2.8 g, range 0.02-12; 5.11-5.84 cm, 1.06-9.20), *Protomyctophum bolini* 0.1, 9.2, *P. normani* 1.0, 28.3, *P. sp.* 0.2, 6.7, unident. Myctophidae 36.2% no., *Notothenia squamifrons* <0.1% no., 2.5% freq., *Paranotothenia magellanica* <0.1, 1.7, unident. fish <0.1, 10.0; cephalopods 13.5% wet wt.: *Moroteuthis* 5.0% freq., 257.0 g (258.4; 23.4-807.2; 19), 0.46 cm LRL (0.12; 0.28-0.69; 19), *Kondakovia longimana* 86.7, 34.0 g (23.0; 5.0-481.0; 933; 90% <261g), 3.1 cm lower rostral length (0.7; 1.8-7.9; 933), unident. Onychoteuthidae <0.2 cm LRL 2.0% no.,

60.8% freq., Onychoteuthidae >0.2 cm LRL 1.7, 29.2, *Gonatus antarcticus* <0.1, 1.7, 13.4 g (16.3; 5.2-52.5; 8), 0.25 cm LRL (0.07; 0.20-0.40; 8), *Histioteuthis* <0.1, 10.0, 68.7 g (13.6; 44.7-94.9; 12), 0.2 cm LRL (0.13; 0.26-0.36; 12), *Alluroteuthis* <0.1, 11.7, 3.6 cm LRL (0.5; 2.6-4.6; 16), *Brachioteuthis* <0.1, 0.8, 0.2 cm LRL (1), *Martialia hyadesi* 7.5% freq., 0.54 cm LRL (0.10; 0.39-0.64; 5), *Galiteuthis glacialis* <0.1% no., 0.8% freq., 55.9 g (15.6; 44.2-73.6; 3), 0.41 cm LRL (0.05; 0.37-0.46; 3), unident. Oegopsida <0.1, 14.2, 0.19 cm LRL (0.07; 0.15-0.33; 36), unident. Teuthoidea <0.1 cm LRL 0.7, 35.0, unident. Teuthoidea >0.1 cm LRL 0.5, 34.2; crustaceans tr. wet mass: amphipods <0.1% no., 6.7% freq., euphausiids <0.1, 1.7, shrimps *Nauticaris marionis* <0.1, 4.2, unident. prawns/shrimps <0.1, 1.7, unident. crustaceans <0.1, 1.7; crustaceans possibly taken first by fish or cephalopods. Took more fish in summer, most cephalopods taken in winter. Proportion of *E. carlesbergi* was particularly low in winter, a peak in *K. anderssoni*/*P. tenisoni* occurred Sept.-Oct. Size of *K. anderssoni*/*P. tenisoni* increased from Mar.-Feb., probably reflecting growth of fish.

At Macquarie I. (118 samples pumped from stomachs, 15031 items; Hindell 1988) fish were *Magnesudis prionosa* 4.5% wt., 0.3% no., 29% freq., *Notolepis* 0.5, <0.1, 3, *Electrona carlesbergi* 71% freq., 6.5 g (9.6; 0.1-29.7; 148), 7.6 cm (2.0-12.0; 148), *Gymnoscopelus* 0.3, 0.3, 3, *Krefflichthys anderssoni* 68% freq.; 2.5 g (1.4; 0.1-7.8; 353), 5.5 cm (19-80; 353), *Protomyctophum* 0.9, 1.0, 22, unident. Myctophidae <0.1, <0.1, 3, unident. fish 0.7, 0.8, 10; cephalopods *Moroteuthis* 38% freq., mean wt. all individuals 32.4 g (52.2; 0.2-578.9; 428), recently ingested individuals 8.0 g (19.9; 0.1-195.6; 136), *Martialia hyadesi* 2% freq., 259.5 g (124.0; 2.7-669.1; 186). *Electrona carlesbergi* was dominant food June-Sept., *K. anderssoni* Oct.-Nov., Jan.-May (no data Dec.), size of both prey species peaking Aug.-Sept.

At Iles Crozet, cephalopods 2-15 cm (36 stomachs; Ridoux *et al.* 1988); earlier sample size 51 stomachs (Barrat 1976). At S. Georgia (Croxall & Prince 1980; Croxall & Lishman 1987; Croxall *et al.* 1988) cephalopods also incl. *Psychroteuthis glacialis*, *Martialia hyadesi* 420 g. Other records: at S. Georgia only cephalopod beaks (Murphy), cephalopods and fish *Notothenia rossii marmorata* (Stonehouse 1960); at Falkland Is, numerous small fish (Murphy).

Table 2. Diet of King Penguin

| | % wt. | | | | % no. | | | % freq. |
|---|-------|------|------|----|-------|------|----|---------|
| | 1 | 2 | 3 | 4 | 1 | 2 | 4 | 5 |
| FISH | 68.7 | 97.8 | 97.7 | 30 | 82.8 | 99.1 | 10 | 10 |
| Myctophidae | | 92.1 | >90 | | 82.6 | 97.9 | | |
| <i>Electrona carlesbergi</i> | | 53.2 | | | 13.2 | 48.5 | | |
| <i>Krefflichthys anderssoni</i> / <i>Protomyctophum tenisoni</i> | | 37.7 | | | 31.8 | 48.1 | | |
| CEPHALOPODS | 31.3 | 2.2 | 2.5 | 70 | 17.1 | 0.9 | 90 | 98 |
| <i>Moroteuthis</i> | | 2.1 | | + | <0.1 | 0.9 | | |
| <i>Kondakovia longimana</i> | | | | + | 12.0 | | | |
| <i>Martialia hyadesi</i> | | <0.1 | | + | <0.1 | <0.1 | | |
| CRUSTACEANS | | + | | | 0.1 | | 2 | |

1. Marion I. (Adams & Klages 1987); 2. Macquarie I. (Hindell 1988); 3. S. Georgia (Croxall & Prince 1980; Croxall & Lishman 1987; Croxall

INTAKE Feeding frequency varies greatly with time of year and between years: at Marion I.; small chicks fed small

amounts frequently by brooding adult; for large chicks, mean feeding interval 4.0 days (0.6; 3.2–5.1; 28; Adams 1987). At Iles Crozet, mean feeding interval (days) in two different years (Barre 1977; Cherel *et al.* 1987):

| Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|------|------|------|------|------|-------|------|------|------|
| 11.2 | 20.9 | 10.4 | 45.6 | 12.5 | 9.4 | 12.6 | 4.8 | 4.8 |
| - | 45.4 | 88.3 | 29.6 | 27.5 | - | 7.4 | 4.6 | 8.2 |

At S. Georgia, chicks fed every 2–3 h in first 3 days; 2–3 times/day during rest of guard-period; every 23 days, June–Sept. (Stonehouse 1960). Other studies: chicks fed every 2.8 days (period unspecified; Croxall *et al.* 1984c); intake, 0.18 meals/chick/adult/day (period unspecified; Croxall & Prince 1987). At Macquarie I., digestion may be complete within c. 4 h; final feed must be obtained within 35 km of colony if adults are to bring food back to chicks (Hindell 1988). Average meal size fed to large chicks: at Marion I., Oct.–Dec., 1152 g (714; 115 stomachs), 1403 g (1235; 11–6012; 120 reconstituted meals), 1650 g (325; 1170–2190; 15 daily chick weighings; Adams & Klages 1987); at Iles Crozet, Apr. 1300 g, May 580, June 730, July 210, Aug. 950, Sept. 850, Oct. 640, Nov., Dec. 1000 (daily chick weighings; Barre *et al.* 1976); at Iles Crozet in Oct.–Dec. of different year 1800 (100; 500–3600; 47 daily chick weighings; Cherel *et al.* 1987). At Macquarie I., mean weight of food recovered from adult penguins reaching shore 923.0 g (518.4; 4.9–2342.0; 144); a further 52.3 g (25.2; 5) estimated to have been left in stomachs after sampling; weight rising from 117.6 g Nov. 1984, peaking at 1186 g Apr. 1985, declining to 763.4 g July, up to 1290.2 g Sept. and decreasing slightly to Nov. At S. Georgia, mean meal size about 2000 g with mean daily weight gain of 130 g (Stonehouse 1960). Chicks' rate of growth highest in summer at Marion I. (Adams & Klages 1987), Iles Crozet (Barrat 1976) and S. Georgia (Stonehouse 1960), probably related to availability of prey (Adams & Klages 1987). On Iles Crozet, fasting in chicks and adults has 3 phases: for first 6–9 days, weight loss rapid, then levels off; protein main source of energy; during second phase (≤ 133 days), when fat main source of energy, protein spared; constant specific loss of weight (mean 6.3 g/kg/day); final phase (≤ 24 days) often lethal, with sharp increase in use of protein and loss of weight. Total loss $\leq 70\%$ of initial weight (Cherel & Maho 1985a,b, 1988; Cherel *et al.* 1987). Assimilation efficiency of energy in cephalopods 81.3% (79.8–84.3; 4; Adams 1984). In captivity has been maintained on 675 g/day of fish (Penfold 1979), 699 g/day cephalopods (Adams 1984), 1400–1700 g/day fish with gain of weight of 100–200 g/day (Copestake *et al.* 1983), or on 1250 g/day euphausiids with gain in weight of 300 g/day (Copestake *et al.* 1983). Lipid contents of stomach contents 3.27–4.57% wet weight (Horgan & Barrett 1985).

SOCIAL ORGANIZATION Highly gregarious at breeding localities throughout year. At sea, in large groups only near colonies. Offshore, in small groups (5–20) when travelling or resting, often solitary when diving for food (J-C. Stahl); in se. Atlantic and sw. Indian Oceans, average of 4.3 birds/survey in 11 10-min survey periods when birds present (Enticott 1986). In colonies, breeding adults segregated from moulting, roosting and unoccupied birds (adults and immatures) in summer; adults and chicks segregated in winter (Murphy; Stonehouse 1960).

BONDS Monogamous. At Iles Crozet, 3.75% ($n=32$) of birds bred with same partner during following season; divorces occurred when arrival of birds poorly synchronized so that traditional breeding sites within colony not uniformly

occupied (Barrat 1976). At S. Georgia, of eleven unsuccessful pairs, seven broke up in next season because one or both partners disappeared, three divorced because arrivals did not coincide, one renewed. Pair-bonds of successful breeders probably not renewed because females stop feeding chick and moult about 1 month earlier than males; once, female settled with new partner while male still feeding chick (Stonehouse 1960). Age at first breeding, 4 years (Barrat 1976). Sex-ratio apparently balanced. Pair-formation starts at return from post-moulting period at sea.

PARENTAL CARE Both parents incubate and tend young continuously until c. 38 days after hatching; then young form crèches for last 9 months of growth. **CO-OPERATIVE BREEDING.** Adults normally feed only their own chick, and crèches not guarded. At S. Georgia, one instance of cooperative breeding among 117 breeders followed throughout cycle; after loss of egg, one female helped feed chick of neighbouring pair until independence. Chicks may also receive small quantities of food or mucus during mock-feeding by unemployed adults during autumn and winter (Stonehouse 1960).

BREEDING DISPERSION Colonial. No nest; eggs incubated on feet of adults. **TERRITORIES.** Adults territorial only during end of courtship, incubation and brooding. Territory mobile, reduced to area within individual pecking distance; however, movements during incubation and brooding limited to few m (Stonehouse 1960; Barrat 1976). At Iles Crozet, density 2.2 territories/m², area 0.46 m², distance between eggs, 0.77 m (Barrat 1976). At Iles Kerguelen, density 1.6 territories/m², area 0.63 m², distance between eggs, 0.89 m (Bauer 1963, 1967). At S. Georgia, density 1.3 territory/m², area 0.79 m², distance between eggs 1 m (Croxall & Prince 1980). At Iles Crozet, 39% ($n=33$) of breeders return to precise location of territory of previous season, 94% to within few metres; no sexual difference in fidelity to breeding-site (Barrat 1976). Outside incubation and early nestling periods, gregariousness varies among adults, which are not then tied to breeding territory. During pair-formation, incubation and chick-feeding, adults aggressive towards neighbours. During bad weather, non-territorial adults and immatures tightly grouped, separated by 20–30 cm, but do not huddle, even in coldest localities, as chicks do within crèches.

ROOSTING Communal on breeding grounds throughout year; immatures and unemployed adults mixed. Roosting mainly nocturnal, but small diurnal loafing groups frequent. Roosting sites at periphery of colonies. Numbers on roosting sites build up gradually during late afternoon and evening; mass departure at dawn (Stonehouse 1960; Barrat 1976). Behaviour at sea unknown during and outside breeding season.

SOCIAL BEHAVIOUR Based on detailed studies at S. Georgia (Stonehouse 1960) and Iles Crozet (Jouventin 1982). Information supplied by J-L. Mougín and J-C. Stahl. Displays conspicuous, easy to observe. Sociable; aggression varies with stage of breeding cycle and weather. Individual distance 0.8–1.0 m during incubation and brooding; reduced to 20–30 cm among groups of unemployed birds during bad weather.

AGONISTIC BEHAVIOUR **THREATS** include: (1) **Ear-rubbing:** displacement preening of shoulder and upper-parts of flippers, denoting low-level aggression in conditions of conflict. (2) **Wing-flapping:** birds flap flippers if alarmed or uneasy; infectious warning posture. (3) **Horizontal Head-circling Motion:** bird throws head back, then moves it

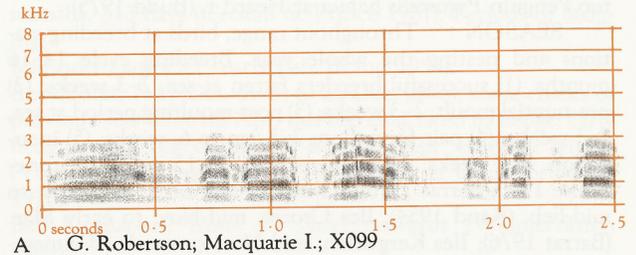
forward in lateral half-circling motion while grunting, highly ritualized, probably denoting intention of movement of striking with bill, and not necessarily directed towards particular individual; often executed by solitary birds. Low-level aggressive posture, rare in birds occupying territories, more frequent outside territories. (4) **Direct-stare Display**: non-ritualized intention movement, in which bird faces opponent, wings raised, bill stretched out. **FIGHTING** rare, but may be seen in birds standing or lying on bellies on nest; use flippers to strike and bill to pinch opponents. **APPEASEMENT: Defence Posture** in which bird moves rapidly among conspecifics, trying to avoid blows by flippers and bills; body outstretched, head held high, bill raised and flippers slightly spread.

SEXUAL BEHAVIOUR ADVERTISEMENT: male advertises presence soon after arrival by calling (Short Call) and **Advertisement Posture**: head lifted, bill nearly vertical, neck fully extended, eyes half closed, flippers held at small angle from body, back slightly concave, and tarso-metatarsi raised from ground; display may be repeated several times with bird standing still during intervals. **Head-flagging**. If advertisement successful in attracting female, the two birds face each other, 1–2 m apart, both shaking heads vigorously in horizontal plane for up to several minutes; displacement activity indicative of conflict; Head-flagging may be punctuated by series of antiphonal short calls from both birds. After period of Head-flagging and calling, one partner (usually male) leads off in **Advertisement Walk** (or **Attraction Walk**): special gait with characteristic pendulum motion of head; followed by partner. Advanced courtship characterized by **High-pointing**: partners face each other, slowly lift heads while contracting muscles of neck, stretch as tall as possible and freeze in this position for 5–10 s or longer; usually initiated by male and may be followed by Head-flagging before birds relax to normal standing posture. Later, engage in **Antiphonal Duets** of Long Calls and **Dabbling**: one bird bends down, imitated by partner; this leads to **COPULATION**: during one of female's bows, male hooks neck over hers and presses downwards or presses bill into feathers of female's neck and head. Female then slides to ground and male mounts with difficulty, steadying himself occasionally by pinching mate's neck with bill and pressing wings against her sides. **Bill-clapping** observed during pre-copulatory bows. Dabbling occurs before and after egg-laying. At change-overs during incubating and brooding, both birds show **Mutual Display** involving antiphonal duets and Dabbling. No courtship feeding. **Mutual Preening** observed, though not often.

RELATIONS WITHIN FAMILY GROUP Both parents take turns in incubation, brooding and feeding chick. Parents recognize chick by voice. Young also recognize parents by call but, if starving, will beg for food from others, generally without results. Fed by regurgitation: during brooding, fed on request; in first few weeks after end of brood-stage, several times a week; during winter, not fed at all; and at end of growth, once or twice a week (details in Food). Chick fledges alone; no dependence on adults after fledging. Normally, adults only attend own chick, will drive away others that beg. During brooding, chick protected from predators by standing on parent's feet. After end of brood-stage, flees from potential danger, trying to join crèche or to place adult between it and predator, thus taking advantage of adult's agonistic behaviour. Can also strike with flippers and pinch with bill; full-grown and healthy chicks successfully thus repel giant-petrels during winter and spring.

VOICE Based on detailed studies by Derenne *et al.* (1979) and Jouventin (1982). Descriptions in Stonehouse (1960) and Murphy. Information supplied by J-L. Mougins and J-C. Stahl. Colonies very noisy between late spring and early autumn; in winter, only whistles of chicks and few adult songs preceding infrequent feeding of chick. Contact Call; rather soft cooing sound audible at great range (>1 km). Agonistic Call: shortened, distorted version of Display Song. Display song (or Long Call): loud polysyllabic trumpeting, not unmusical; short call, abbreviated version of it. Call of chicks, clear three-note whistle. Call by day or night on colonies and at sea. **SEXUAL DIFFERENCES** in display-song, more highly pitched and cut into more numerous and shorter syllables in females than in males. **INDIVIDUAL DIFFERENCES** in number of syllables, total length and principal frequency. Some **GEOGRAPHICAL VARIATION** indicated: Iles Crozet, Kerguelen and Macquarie I. songs identical; songs of Falkland Is birds last 2 s longer and contain more syllables. **NON-VOCAL SOUNDS**: Bill-clapping during pre-copulatory bows; clattering of flippers at sea. Alarm signal after detection of predators, e.g. Leopard Seal (Stonehouse 1960).

ADULT DISPLAY SONG: loud, polysyllabic trumpeting (sonagram A); not unmusical; emitted with Advertisement



Posture. Two Display Songs described: **Short Call** and **Long Call**; mean duration of each at Iles Crozet were, respectively, 2.62 s (0.8; 1.5–5; 50) and 3.47 (0.84; 2–5.4; 50); however, duration of Short and Long Calls overlap sometimes, which makes distinction difficult. Short Calls emitted by solitary birds searching for mate at beginning of courtship; sex of calling bird is only information conveyed; mostly confined to period of pair-formation. Long Calls used for individual recognition between partners and between parent and chick; uttered whenever bird needs to be identified. Considerable variation between Long Calls of different individuals, but all calls of individual nearly identical, even from one year to next: signal duration, syllable number and length, nearly constant. Distinct sexual differences: female songs have mean of 12.0 syllables (8–18), male songs only 9.3 (6–13); female songs also more highly pitched, mean main frequency 2937 Hz (2750–3500 Hz), for males 2400 Hz (1000–3800 Hz); mean maximum frequency for females 6781 Hz (6000–7000 Hz), for males 6200 Hz (4000–8000 Hz). Length of song not very different: females 3.33 s (2.42–4.45), males 3.69 (2.20–5.20). Consequently, length of syllables greater among males. Even though most singing birds can be sexed by human ears, not perfectly reliable because some overlap in number of syllables and frequency. **Agonistic Call** resembles shortened display-song, but distorted and highly varying with unique characteristic pattern. Not associated with ritualized posture. Generally emitted just before pecking. **Contact Call**: rather soft cooing, frequency ranges between 250 and 5000 Hz, maximal intensity c. 1000 Hz, duration between 0.4 and 0.8 s. Call uttered by single birds, bill pointed upwards. Used to signal and locate

position of individuals or groups on land and mostly at sea; **Alarm Call** and **Bathing Call** seem to be mere variants of Contact Call.

YOUNG Chicks utter one call: modulated whistle varying in amplitude and frequency; dominant frequency about 2000 Hz, frequency band extending over 1.5 Hz; duration less than half a second; call consists of three repeated whistles; call becomes more highly pitched and varies more when chick frightened. Structure of calls of individual chicks do not vary; however, much variation in calls between chicks. Structure of call established shortly after hatching and does not change until end of growth. Call used for individual recognition by parents and begging for food. Parent-chick duet forms basis of individual recognition as calls do not vary (whereas appearance of chick certainly changes between two feeding trips).

BREEDING Fairly well known. Most comprehensive studies at S. Georgia (Stonehouse 1960) and Iles Crozet (Barrat 1976). Information supplied by J-L. Mougin and J-C. Stahl. Breed colonially on islands in Subantarctic and low Antarctic Zones, usually on coastal lowlands, often near mouths of streams. Not associated with other species, except with Gentoo Penguin *Pygoscelis papua* at Heard I. (Budd 1975).

SEASON Throughout range, birds at breeding stations and nesting the whole year. Breeding cycle 14–16 months: (1) successful breeders fatten at sea, 2–3 weeks; (2) pre-nuptial moult, 2–3 weeks; (3) post-moulting period at sea, 2–3 weeks; (4) pair-formation, 2–3, up to 6, weeks; (5) incubation, c. 8 weeks; (6) chick-rearing, 10–13 months (Stonehouse 1960; Barrat 1976). Laying: at Marion I., end Nov. to mid-Feb. (Rand 1954); Iles Crozet, mid-Nov. to early Mar. (Barrat 1976); Iles Kerguelen, end Nov. onwards (Weimerskirch *et al.* 1989); Macquarie I., end Nov. to early Jan. (Falla 1937); S. Georgia, end Nov. to mid-Apr. (Stonehouse 1960); Falkland Is, Nov.–Dec. (Woods 1975). Constant from year to year but may vary from colony to colony. Breeding frequency not clearly known but certainly not annual. Sequence for successful breeders inferred from data gathered during one year and not substantiated by dates of laying or by frequency and breeding success. At S. Georgia, likely sequence for potentially successful pair: first early laying leading to successful fledging, end Nov. to early Jan.; next later successful laying, mid-Jan. to mid-Feb. or 12–14 months after first; next attempted laying end Feb. onwards or 12+ months after second, doomed to failure; then return to early successful laying in Nov. or c. 6 months after third. Thus, at best only two chicks can be reared in three years. But return of successful females c. 1 month before males and possible re-laying during same season complicate or confuse the matter (Stonehouse 1960). At Iles Crozet, total and effective laying period (mid-Nov. to mid-

Jan.) shorter than at S. Georgia and laying dates of unsuccessful breeders (3 Dec.–22 Jan.; 16) earlier and longer. Sequence seems to be biennial rather than triennial, with successful breeding in one year followed by unsuccessful the next, except perhaps by earliest returning successful breeders (Barrat 1976).

SITE Most colonies not far from sea (10s–100s m) and near sea-level; on gently sloping beaches or at mouths of valleys on rather large level areas, protected against winds (Barrat 1976; Falla 1937; Stonehouse 1960). Vegetation much suppressed by trampling birds but some, mostly tussock-grass *Poa* spp, may survive within colony; ponds, lakes and rivers may also occur near or in colony but neither vegetation nor water important for establishment of colony. Colonies occasionally on inland hills, 100+ m asl and 1500 m from sea; e.g. at Ile aux Cochons, Iles Crozet, the biggest known colony (2x10⁵ pairs; Derenne *et al.* 1976) and in S. Georgia (Matthews 1929), on level and on steep ground. If necessary, birds maintain wide (several m) paths through high thick vegetation as access to and from sea. At Marion I., colonies just above high water mark, and not on slopes or inner plain; but on Iles Crozet, large colony on inland hills >100 m asl and 1500 m from sea. Colonies on valleys and beaches of Heard I. sheltered and sunny, in lee of mountains; moraine colonies on windward coast, but wind-speed at sites of colonies lower than in nearby areas. At S. Georgia, colonies on moraines exposed to cold winds. Sites may be devoid of vegetation; on Marion I. and Macquarie I., nest on beaches of stones embedded in mud and guano where water drains easily; avoid sandy beaches, and grassy, mossy or wet ground; boulder-covered beaches also avoided, but used at Heard I. At S. Georgia, early breeders settle on dry ground, but later pairs are forced into surrounding tussock grass *Poa cookii* (Stonehouse 1960). Colonies on Heard I., among tussock grass and *Azorella selago* or in patches of lush grass among coarse grass and Kerguelen cabbage *Pringlea antiscorbutica*.

NEST, MATERIALS Nil. Egg incubated on feet of adults. Birds remain strictly at site of laying and do not walk about carrying egg. Slight shifts, at most a few metres, may be caused by intrusion of new breeders or departures of unsuccessful ones.

EGGS Pyriform; smooth textured; pale greenish white, usually with white chalky coating.

MEASUREMENTS:

Iles Crozet 104.1 (92.9–124.0; 291) x 73.9 (61.2–87.0)
S. Georgia 104.8 (86–117; 75) x 76.0 (64–86) (Murphy)
Marion I. 105.8 (93.8–112.5; 35) x 74.0 mm (65.2–79.0) (Rand 1954)

Macquarie I. 100.7 (91–106; 15) x 73.9 mm (69.5–78.0) (Wilson 1907; Oliver)

WEIGHTS:

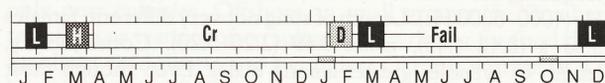
Iles Crozet 302 (235–380; 186)

S. Georgia 319 (205–440; 75)

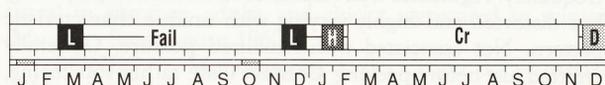
Marion I. 304 (243–351; 16).

CLUTCH-SIZE Usually one. Some replacement laying. At S. Georgia, out of 40+ birds, 4 females and 10 males lost egg before end Dec., bred again, re-laying within 39–c. 45 days (n=3) of loss, including 3 weeks at sea (Stonehouse 1960).

LAYING Poorly synchronized at all localities. At S. Georgia: between 25 Nov. (in two seasons) and mid-Apr. (in one season) in two waves with maxima in second week Dec. and early Feb., representing 23–26% early breeders, c. 10% intermediate breeders, c. 34–39% late breeders, and 25–33%



a). sequence from a late, successful attempt



b). sequence from a very late, failed attempt

ineffective breeders (Stonehouse 1960); Croxall & Prince (1987) gave laying period as Dec. to 21 Feb. At Iles Crozet: laying (eight eggs) began 10–23 Nov., ended (seven eggs) 21 Feb.–12 Mar. (Voisin 1971; Barre 1977; Derenne *et al.* 1976) and distribution unimodal with maximum in Dec. Egg laid at any hour of day or night.

INCUBATION By both parents alternately. At S. Georgia: female leaves 1 day (0–2; 4) after laying, having fasted for 14.9 days on average and lost c. 26% weight; then incubation as follows: male, 18.6 days (16–22; 7), having fasted for 37.7 days and lost nearly 40% weight; female, 18.7 days (17.5–21; 6); male, 12.2 days (10–14.5; 8), when sometimes egg hatches; female, 9.9 days (8–12; 13), when most eggs hatch, 4.3 days into stint (0–9; 11; Stonehouse 1960). At Iles Crozet, routine similar: female leaves egg after a few hours; then, male, 16.8 days (12–22; 19); female, 18.3 days (14–23; 19); male, 14.8 days (11–20; 19), fewer than half eggs hatching during this stint; female, 10.1 days (7.0–14.1; 18) with most eggs hatching 5.2 days (1–13; 11) into this stint (Barrat 1976). Thus males take somewhat greater share (56–60%) of incubation than females. Parents do not recognize own egg and do not help hatching, except fortuitously. Daily loss of weight of both sexes during incubation c. 153 g or c. 1.07% of initial weight (Stonehouse 1960). **INCUBATION PERIOD:** S. Georgia, 54.5 days (53–57; 11); Iles Crozet, 53.2 days (52–54; 20). Added eggs incubated for up to 87 days (Barrat 1976).

NESTLING Semi-altricial, nidicolous. Nearly naked at hatching. After three weeks covered with brownish down; facial mask and neck, light grey. First sign of teleoptile plumage normally appears from end Sept. Moulting begins with replacement of tail-feathers; down lost in upward progression within last 10 days of moult, which lasts for about 6 weeks in all (Barrat 1976). Chick brooded by both sexes alternately in decreasing stints. At S. Georgia: total length of brood-stage, 39.0 days (4.6; 30–44; 12), shared in an average of 8.3 stints (6–11), for males lasting 5.0 days (1.8; 3–10; 45) and for females 4.4 days (1.2; 2–7; 43). In Iles Crozet, homeothermy achieved at c. 20 days old (Barre 1978) but brood-stage lasts for 32.8 days (28.5–37.5; 13) (Barrat 1976); av. number of stints 4.8 (max. 7), lasting on average 6.8 days, i.e. fewer but longer stints than at S. Georgia. On Marion I., stints averaged 12.8 days (5.4; 4–21; 28), much longer than elsewhere (Adams 1987). At end of brood-stage, chicks left alone and gather into crèches for nine months or more till they fledge. Both parents feed only their own chick, by incomplete regurgitation. During winter, parents stay ashore with their chick for 1.9 days (0.5; 1–11; 20) at Iles Crozet (Cherel *et al.* 1987); at S. Georgia for periods of 2–3 weeks. Crèches not guarded by adults; chicks defend themselves against predators.

GROWTH Three distinct periods: (1) **Initial growth** (hatching to mid-Apr. to early May). Weight at hatching: S. Georgia, 220 g (n=10); Iles Crozet, 226 (190–275; 25). Growth, exponential for first 20 days, then decreasing. Mean daily gain: S. Georgia, 33 (15%) for first week and 223 (5.2%) in sixth week (n=10); Iles Crozet, 30 (13%) for first week and 216 (4.9%) in sixth (n=25). Length and weight reached at end of this period depends on date of hatching: at Iles Crozet, early chicks (n=12) reached 12.1 kg in about 3 months (Cherel & Le Maho 1985); at S. Georgia, chicks (n=12) hatched late Jan. reached mean maximum weight of 12.0 kg. (2) **Winter starvation** (Apr.–May to Sept.–Oct.). At S. Georgia, during 19 weeks, mean total loss of weight 3.8 kg at c. 25 g/day; mean minimum weight reached 8.2 kg (n=6). At Iles Crozet, during 147 days (138–175), mean total loss of weight, 5.6 kg (3.6–7.3)

at 36 g/day (25.7–42.8); mean minimum weight 5.2 kg (3.9–6.1; 8). Lethal minimum weight: at S. Georgia, 3.2 kg (n=89); at Iles Crozet, 2.9 kg (n=11; Cherel *et al.* 1987). (3) **Final growth and moult** (Sept.–Oct. to fledging). At S. Georgia, during 8–9 weeks, mean total gain of weight 2.9 kg at c. 64 g/day; mean weight at fledging, 10.8 kg or 79% adult mass, after loss of 0.3 kg in last two weeks (n=6). At Iles Crozet, during 79 days (51–93) to onset of moult, mean total gain, 6.7 kg (5.2–7.8) at 85 g/day (n=3); mean weight at start of moult, 11.0 kg (7.3–13.3; 18) (Cherel *et al.* 1987); during moult, chicks lose 35.9 g/day despite being fed; mean weight at fledging, 9.0 kg (7.5–10.9; 40) or 75% of adult mass. At S. Georgia, chicks fed by only one parent after May–June, grew more slowly than others but some reached start of moult and probably fledged. Usually females stop feeding chicks about a month before males (Stonehouse 1960). If chicks forced to fast, moult stops (Barre 1977). During Period (1), stature increases rapidly; foot reaches full size. Growth of bill and flipper stops during Period (2) and starts again in Period (3). At fledging, bill 87% of adult size; flipper and foot, 96%. Adult size not reached when two years old (Barrat 1976).

FLEDGING TO MATURITY Chick-rearing period: at Iles Crozet, c. 50 weeks (n=3); at S. Georgia, 10–13 months, 313 days (Croxall & Prince 1987). Periods of fledging:

Marion I., late Oct.–early Feb. (Rand 1954).

Iles Crozet, 7–17 Oct. (n=5) to 25 Dec. (n=6); some chicks of previous year alive till Apr. but too emaciated to fledge; early fledging rare but occasional from 15 Apr. through winter (Voisin 1971; Despin *et al.* 1972; Barre *et al.* 1976; Barrat 1976).

Iles Kerguelen, from 25 Nov. onwards (Weimerskirch 1989)

S. Georgia, begins late Nov.; 30 Dec.–25 Feb. (Croxall & Prince 1987).

At departure completely independent of parents. Annual moult carried out anywhere, sometimes in natal colony. Little knowledge of age at first return to colony or at first breeding: at Iles Crozet, youngest birds returned when 2 years old (= 1 year in colony and 1 at sea) and youngest breeders aged 4 years. Has bred at 2 years old in captivity (Lange 1976). Annual adult survival in S. Georgia 79.8% of 128 banded birds (79.4% of 68 males and 81.7% of 60 females); at Iles Crozet, 82.1% of 56 banded birds had average longevity of 4.5–5.1 years. Survival almost surely underestimated in view of other demographic factors; underestimates probably caused by loss of bands.

SUCCESS Poorly known. At S. Georgia, 2500+ eggs produced c. 2100 chicks at end of growth or 84% total success. On Iles Crozet, of 42 eggs laid, hatching success 27 (64.3%): 27/42 laid before 10 Jan., hatched 77.8% and 15, laid 10 Jan.–12 Feb., 40%. Survival of chicks: of 27, from hatching to end brood-stage, 23 (85.2%) survived (Barrat 1976); of 186, from end brood-stage to fledging, 94 (50.5%) fledged, one third dying Apr.–May and one-quarter in Oct. (Cherel *et al.* 1987); total fledging success, 43%. Of 6 late chicks, hatched after 5 Mar., only one survived to Sept., others all dying before mid-July (Barrat 1976). Of c. 80 000 eggs and chicks on 17 Mar., 28 000 chicks (35%) alive 6 Sept. (Voisin 1971). At Heard I., of 17 eggs and chicks on 17 Mar., only one chick alive and fledging 27 Nov., poor success probably because colony small (Budd 1975). At Macquarie I., total success until mid-Aug. c. 47%; as low as c. 36% in some years (Rounsevell & Copson 1982). Loss of eggs chiefly caused by desertion in early

incubation or by delayed return of partner. At Iles Crozet, up to 10% eggs washed away by waves or floods during storms (Despin *et al.* 1972; Barrat 1976). Skuas *Catharacta* and sheathbills *Chionis* spp take eggs and small chicks. Older chicks die from starvation or killed by giant-petrels *Macronectes* spp. Once, tens of full-grown chicks died during hot weather ($>20^{\circ}\text{C}$) (J-C. Stahl). Success much depends on laying date but relation imperfectly known (Stonehouse 1960; Barrat 1976). At present, unaffected by human activities, except near occupied scientific winter bases.

PLUMAGES

ADULT Definitive basic; acquired at beginning of third year (Stonehouse 1960). Adolescent period until birds at least four or five years old. Sexes similar; females often get muddy breast during copulation. **HEAD AND NECK.** Head and throat, black (89); feathers, black (89) with brown (119B) bases, occasionally visible when feathers ruffled. Throat and midline of crown have green (51) gloss from feathers with narrow bottle-green iridescent tip; green gloss lost with wear. Sides of neck have large yellow-orange patch, shaped like comma, with tails almost meeting on foreneck; becomes paler with wear but cannot be confused with neck-patch of juveniles. Feathers concave; white merges through shades of orange-yellow to orange tip. Black (89) posterior margin to neck-patch separates it from silver-grey hindneck; this margin becomes narrower, and can be lost with wear. Hindneck forms almost complete collar, but centre of foreneck, deep rufous-orange. **UPPERPARTS,** appear black, extensively mottled by short silvery streaks. Feathers have broad flat rachis, brown-horn (91) with black (89) tip. Narrow pennaceous tip, pale silvery grey (c88); with wear, tips shortened, so dorsum may appear spotted, rather than streaked, silver. Open pennaceous areas near rachis, brown-black; open pennaceous feather-edges, light grey-brown (119C) and occasionally visible in moulting birds. **TAIL,** black (89) with fine white tips, rapidly lost with wear. **UNDERPARTS.** Upper breast, yellow (55) merging through shades of orange into foreneck. Rest of underparts, white. Underparts separated from upperparts by continuation of posterior margin of ear-patch; this black (82-89) line runs under flippers, broadest near breast. **FLIPPER.** Upperside as upperparts, occasionally with narrow white trailing-edge; underside, mostly white, bordered black-grey (as upperparts) on leading-edge, base and tip, with short blackish line running towards body from tip. Width of this line varies, and entire flipper-tip may be black.

DOWNY YOUNG Almost naked at hatching, with leathery dark-grey (82-83) skin and single strand of fine grey (-) or black down (-) from each papilla. Replacement of this down begins in first week; at 10 days, chicks have short thick covering of grey-brown (119A-119B) down; filaments on face and neck have pale-grey tips forming indistinct facial mask. At 12 weeks, down long (up to 8 cm) and uniform brown (119A-119B); unclear whether this is mesoptile. This down (or possibly others of identical appearance) retained for up to one year; towards end of this period, can fade to streaky golden brown, with pale-cinnamon to yellowish (c123D) tips to filaments.

JUVENILE Acquired at 10-13 months (Stonehouse 1960); lost at beginning of third year. Neck-patch, usually yellow (55) with no trace of orange; when fresh, appears dull orange-yellow; when worn, exposure of white bases of feathers can make it appear pale yellow to yellowish white. Feathers of crown have narrow blue-grey (88) fringe when fresh. Otherwise, as adult. Published statements (e.g. Lindsey 1986)

that this is immature plumage and juveniles have white throat are incorrect (Falla 1937; Stonehouse 1960; large series of photos from Macquarie I. and Iles Crozet).

BARE PARTS Based on Murphy, Stonehouse (1960) and photos from Lindsey (1986), Peterson (1979) and J-C. Stahl.

ADULT Iris, fawn (25) to dark grey-brown. Mandibular plates range through pinkish (c7) to orange (c16); usually salmon-orange. Anterior end of mandibular plates, mauve (-). Colour not related to age of plate (Stonehouse 1960). Rest of bill, blackish (82). Occasionally juvenile mandibular plates retained for few weeks after post-juvenile moult (Stonehouse 1960). Tarsus and feet, dark grey.

JUVENILE Mandibular plates, black, with varying amount of pink (-) streaking. Entirely black in birds with remnant down. Otherwise, as adult.

DOWNY YOUNG Mandibular plates, blackish (82). Bare skin round eye, grey (84). Iris perhaps paler than adult (Crawford 1952).

MOULTS Based chiefly on nominate *patagonicus* at S. Georgia. Less detailed studies of race *halli* (Barrat 1976; Rand 1955) apparently agree.

ADULT POST-BREEDING Pre-basic. Complete: rectrices are first feathers to be shed; some feathers of crown and back cannot be reached during preening and are last to be shed. Mandibular plates replaced 1-2 months after feather-moult complete. Duration ashore 27-36 days. Unsuccessful breeders begin moult between early Sept. and early Nov. Successful breeders put on fat at sea for one month after abandoning chicks and begin to moult in Dec. or even later.

POST-JUVENILE Begins late Dec. or Jan. at end of second year (Barrat 1976).

MEASUREMENTS (1) Macquarie I., adults, skins; FLIP (A) = flipper from axilla; BILL (P) from tip to base of mandibular plate (MV). (2) Golfe du Morbihan, Iles Kerguelen; methods and ages unknown (Viot 1987). (3) Iles Crozet; methods and ages unknown (Viot 1987). (4) Iles Crozet, adults, live (Barrat 1976). (5) Iles Crozet, adults, live (Barrat 1976). (6) Iles Crozet, three-year olds, live (Barrat 1976). (7) Iles Crozet, juveniles, live (Barrat 1976). (8) S. Georgia, skins (Barrat 1976). (9) S. Georgia, adults, live; BILL (G) from gape to tip; FOOT from 'heel' to end of middle claw.

| | MALES | FEMALES |
|----------|----------------------------------|------------------------------|
| FLIP (A) | (1) 292 (12.6; 267-301; 5) | 298 (8.8; 286-309; 5) |
| | (4) 360 (347-373; 23) | 353 (335-378; 22) ** |
| | (9) 341 (10.0; 323-366; 25) | 329 (8.4; 310-342; 25) |
| BILL | (1) 83.9 (3.52; 78.6-87.2; 5) | 82.6 (2.59; 78.2-85.9; 5) |
| BILL (G) | (9) 136.9 (5.55; 123-149; 25) | 127.6 (5.37; 116-142; 25) ** |
| BILL (P) | (1) 114.9 (3.37; 110.5-118.8; 5) | 114.1 (2.96; 109.6-118; 5) |
| | (4) 125 (117-132; 23) | 119 (109-127; 22) |
| FOOT | (9) 185.6 (6.61; 175-200; 25) | 177.6 (67.8; 166-192; 25) |
| TOE | (1) 99.2 (2.72; 93.8-100.9; 5) | 99.6 (6.88; 92.0-110.8; 4) |
| | (4) 132 (122-140; 23) | 129 (121-138; 22) |
| UNSEXED | | |
| FLIP(A) | (5) 360 (330-390; 199) | |
| | (6) 346 (324-378; 29) | |
| | (7) 346 (321-370; 40) | |

| | | |
|----------|-----------|----------------|
| FLIP | (2) 325 | (10, 51) |
| | (3) 378 | (3; 50) |
| BILL | (2) 87.6 | (4.9; 51) |
| | (3) 92.3 | (6.7; 50) |
| BILL (P) | (5) 122 | (109-135; 199) |
| | (6) 112 | (101-124; 29) |
| | (7) 106 | (97-114; 40) |
| | (8) 130.3 | (126-139; 6) |
| TOE | (5) 131 | (118-145; 199) |
| | (6) 128 | (119-138; 29) |
| | (7) 126 | (117-141; 40) |

WEIGHTS Weights in kg. Breeding adults at Iles Crozet (Barrat 1976): males 12.8 (10.5-15.7; 7); females 11.5 (9.3-12.5; 10). Unsexed adults, Iles Crozet: 12.1 (14.9; 8.9-18); unsexed juveniles: 9.0 (7.5-10.9; 4) (Barrat 1976). See Barrat (1976) for information on variation in weight through year. In S. Georgia, at start of courtship: males 16.0 (11.7; 13.0-17.3; 8); females 14.1 (0.96; 13.1-15.6; 11). At end of courtship: females 10.6 (0.55; 9.7-11.2; 5). Pre-moult: 19-21; post moult: <11 kg. Weight loss about 0.3 kg/day during moult, 0.07-0.21 during incubation (Stonehouse 1960). See Stonehouse (1960) and Cherel & Le Maho (1988) for more information on loss of weight during fasting.

STRUCTURE Uncrested. Bill, long and narrow; both mandibles downcurved at tip. Large plate covers most of base of lower mandible. Feathers encroach onto about one-third of culmen. Tail, short; 20 feathers. Tibia feathered, tarsus unfeathered. Pupil, square when contracted, polygonal when dilated.

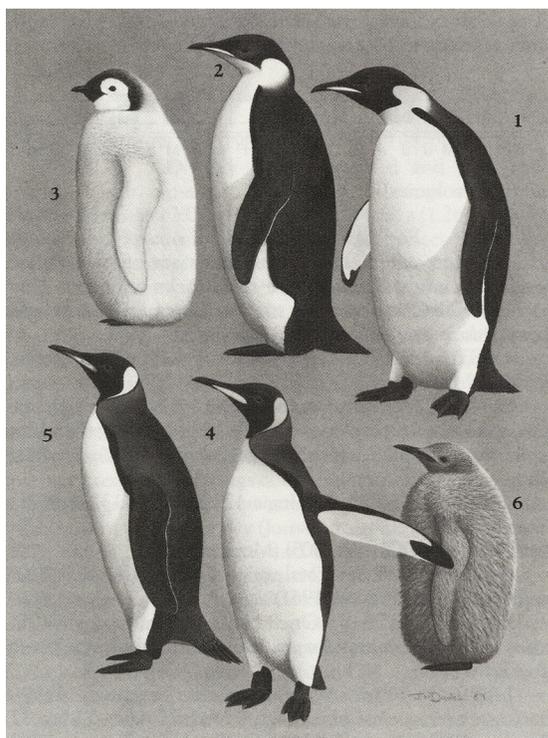
GEOGRAPHICAL VARIATION Slight, if any. Bills and flippers of birds from Iles Kerguelen significantly smaller than those from Iles Crozet; Viot (1987) found genetic differentiation between Kerguelen and Crozet birds, using electrophoresis and biometrics.

DIR

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Volume 1 (Part A), 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

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