

Order SPHENISCIFORMES

Family SPHENISCIDAE penguins

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

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

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

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

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

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

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

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

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

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

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

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

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

REFERENCES

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Rijke, R.M. 1970. *J. Exp. Biol.* 52: 469-79.
- Simpson, G.G. 1975. Pp 19-41. In: Stonehouse. 1975.
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Eudyptes robustus Oliver, 1953, *Emu* 53: 187 — Snares Islands.

Robustus (stout) refers to the bill, which is even more robust than that of Fiordland Penguin *E. pachyrhynchus*.

OTHER ENGLISH NAMES. Snares Crested Penguin, Snares Island, Snares Island Crested Penguin.

The epithet **Snares** denotes the only known breeding locality for the species.

MONOTYPIC.

FIELD IDENTIFICATION Length 51–61 cm; flipper 17–20 cm; bill 48–69 mm; weight: male 3.4 kg, female 2.8 kg. Medium-sized, stocky penguin with large bulbous orange bill. Bright yellow superciliary stripe starts near nostril and forms laterally projecting or drooping crest behind eye. Prominent bare skin at base of bill. Sexes alike but distinguishable by size, especially of bill. No seasonal changes. Juveniles and immatures separable.

DESCRIPTION **ADULT.** Head, blackish with conspicuous narrow bright-yellow superciliary stripe, starting near junction of culminicorn and latericorn; stripe extends horizontally over eye to back of head where it develops into long silky plumes (> 5 cm) that flare out from head and droop down sides of nape. Viewed from front, superciliary stripes form V diverging from base of bill. Cheek feathers, blackish, rarely showing pale bases when spread. Flippers, blue-black dorsally with thin white trailing-edge. Dorsal plumage and tail, black. Sharp demarcation across throat separates black face from silky white breast and abdomen. Underflipper, whitish with dark tip and posterior base; blackish strip extends for varying distance along leading-edge from base. Bill, large and heavy, orange-brown, with noticeably bulbous culminicorn when viewed from above or from side. Base of culminicorn on old birds often has transverse series of ridges and grooves. Prominent pinky-white bare skin separates base of latericorn and mandible from feathers; bare triangle of skin especially noticeable at gape. Narrow strip of blackish skin separates base of culminicorn from feathers. Eye, usually bright reddish-brown, but varies; in some, pinkish or even pale yellow-brown. Feet and legs, pinkish white above and blackish brown behind tarsi, soles and front of webs. Claws, dark brown. Before moult (Mar.), dorsal feathers become brownish and superciliary stripe and crest fade to pale yellow. Immediately after moult (May), dorsal feathers shiny with strong bluish cast. At sea, look for large orange bill, pink skin at base of bill, dark cheeks and thin superciliary stripe running from naricorn horizontally over eye. Crests lie flat against head when wet. **FLEDGELING.** Smaller than adult. Superciliary stripes,

yellow and clearly defined but crests short and only slightly spread posteriorly. Chin colour varies from blue-grey to pale grey; feathers, often grey with dark tips, thus becoming lighter with wear. Dorsal plumage, dark blue. Bill smaller than adult; blackish-brown with slight gloss and paler distally with small horn-coloured tip to maxilla and mandible. Bill much less robust than adult, tapering from base to tip. Thin strip of pink skin round base of latericorn and ramicorn not so prominent as adult but noticeable at gape. Eye, dull brown. Feet and claws, as adult. **ONE-YEAR-OLD.** Smaller than adult. Superciliary stripe pale yellow; crest poorly developed. Chin usually grey but sometimes whitish; occasionally nearly black. Dorsal plumage brown-black. Bill less robust than adult, dull orange-brown with darker shading, especially at base and tip. Culminicorn may appear parallel-sided (as in adult Erect-crested Penguin) when viewed from above. Thin fleshy margin to bill present but not conspicuous. Eye, dull grey-brown or chocolate brown. Before moult (Jan.), yearlings appear almost brown on back and superciliary stripe almost white. Most stragglers are of this age group. Some moulting immatures have broad pale superciliary stripe as feathers loosen, appearing more like Fiordland Penguin, but check for larger bill and presence of bare skin at base of bill. After moulting, yearlings small and slim with short, bright-yellow crests, dark chin and throat, and shiny blue-black dorsal plumage. Birds-of-year difficult to identify at sea, but look for clearly defined narrow superciliary stripe that starts near naricorn and passes back horizontally over eye. Also look for bare skin at base of bill. **TWO-YEAR-OLD.** As adult but crests shorter and bill duller and less robust. Usually moult Feb.-mid Mar. **THREE-YEAR-OLD.** Very similar to adult, but crests not fully developed. Moult Feb.-Mar.

SIMILAR SPECIES Average size for genus. Similar to Fiordland Penguin *E. pachyrhynchus* but larger than Rockhopper Penguin *E. chrysocome* and smaller than Erect-crested *E. sclateri* and Macaroni *E. chrysolophus*. Most similar to Fiordland and Erect-crested Penguins but resembles all other crested penguins. **ADULT.** **Fiordland** has shorter, less robust bill and lacks bare pink skin at base of bill. Superciliary stripes

broader, paler yellow and crest-feathers usually shorter. Cheek-feathers with pale bases that often show as whitish stripes radiating out from base of bill. Often appears dumpy. More timid than Snares Penguin. **Erect-crested**, taller with less robust, brownish bill; culmen straight-sided when viewed from above and from side. Superciliary stripe starts near gape and rises obliquely over eye. Crests erectile, brushy and nearly parallel when seen from front or above (diverge from bill in Snares). Head, dome-shaped, velvet-black; characteristic large-chinned appearance in profile. Markings on underside of flipper bolder. **Rockhopper**, smaller with much smaller bill. Bare skin at base of bill less prominent or absent; eye, bright red. Superciliary stripe starts further back from bill, very narrow until behind eye. Crests long and fibrous, including more black feathers, and joined by black occipital crest. **Macaroni** and **Royal**, taller, with longer, more massive bills and very prominent dark-pink skin at base of bill and at gape. Chrome-yellow fibrous crest feathers meet as yellow-orange patch on forehead. No clearly defined superciliary stripe. **JUVENILE. One-year-old Fiordland**, dumper, with smaller bill that lacks fleshy margins. Superciliary stripes broader, almost white. Face usually paler grey, often almost white; dorsal plumage browner. **Erect-crested**, taller and more gangly, bill duller brown and less bulbous. Superciliary stripe, pale yellow, rising obliquely from near gape. Superciliary stripes appear parallel when viewed from front. Large grey chin extends further out towards bill tip. Markings on underside of flipper bolder. **Rockhopper**, smaller with tiny bill, and thin, poorly developed superciliary stripe that starts 1–2 cm back from naricorn. Eye redder, and black occipital crest already noticeable. **Macaroni** and **Royal**, taller, with long slim bills and bright-pink triangle of skin at gape. Indistinct superciliary stripe, but messy patch of chrome-yellow and white feathers on forehead.

Breed in small to medium-sized colonies at Snares Is. Absent from breeding grounds from May to Sept. but movements unknown. Usually walk on land but hop when hurried. Will toboggan if panicked. Swim with head and part of back above water; porpoise when swimming fast. Usually encountered in small groups at sea. Vagrants solitary or among other crested penguins. Voice harsher than Fiordland Penguin, more highly pitched and much harsher than Erect-crested.

HABITAT Cool temperate and subantarctic waters round sole breeding station, Snares Is. During breeding season, mainly found near coast; thought to feed in inshore waters as chicks fed frequently (J. Warham). Feeding flocks seen over tidal rips (C.M. Miskelly). Assumed to be pelagic outside breeding season but range poorly known. May feed along Subtropical Convergence in areas of upwelling (Warham 1975).

Most colonies in flat nuddy areas or on gentle rock slopes; up to 600 m from shore and 70 m asl. Situated under canopy of *Olearia lyallii* or *Brachyglottis stewartiae* forest, among thickets of *Hebe elliptica*, in open swampy areas, on exposed granite, or among rock falls. Shade provided by vegetation is important to nesting birds, and colonies among *Hebe* change shape and position as vegetation killed by trampling, guano deposition (Fineran 1964; Stonehouse 1971; Warham 1974a); colonies under *Olearia* and *Brachyglottis* usually stable.

Landing places are granite points or slopes on more sheltered e. side of islands (Warham 1974a; Miskelly 1984). Route

to colony generally beside watercourse and may be steep (Stead 1948). Breeding adults moult at nest-sites (Warham 1974a); non-breeding birds gather during moult at fringes of colonies and on bare rock above landing areas; moulting immatures occur away from Snares Is on rocky coasts and in sea caves. Shallow dives (<5 m) used to catch surface-swarming crustaceans; maximum diving depth not known.

DISTRIBUTION AND POPULATION Endemic to NZ. Breed Snares Is. Ranges to mainland NZ (usually S of Akaroa, Banks Pen.); Stewart I.; Solander I.; Chatham Is; E to Antipodes I. Vagrant Aust. and Macquarie I.

Away from Snares Is, records mainly of moulting immatures in Jan.–Feb. After completion of moult, Snares Is deserted until return of first males in late Aug. (Horning & Horning 1974; Warham 1974a). Wintering range unknown; paucity of sightings (one record Otago, NZ, and three records Tas.; see below) suggests winter range well away from land and possibly towards Aust.

AUST. **Tas.:** singles: Seven Mile Beach near Hobart, 27 Aug. 1951 (Tas. Mus.: B2637/10002; Simpson & McEvey 1972); 16 Apr. 1987 (Tas. Bird Rep. 1988); S. Bruny I., 11 Feb. 1977 (Tas. Bird Rep. 1979); Port Arthur, 26 Aug. 1978 (Aust. Atlas); Ravensdale, 19 June 1979 (Aust. Atlas); Safety Cove, 17 Nov. 1985 (Tas. Bird Rep. 1986). **SA:** near Cape Banks, 8 Jan. 1914 (SAM: B1071; Simpson & McEvey 1972).

NZ **NI:** one record, single bird moulting, n. side Cook Str., Jan. 1972 (CSN 19). **SI:** Otago, at least seven records in Jan. and Feb. (CSN 20, 24); one winter record, 27 July 1971 (CSN 19). Three records Southland: Te Waewae Bay, Waiau R. mouth, 6 Mar. 1968 (Robertson 1972); beachcast, Jan. 1963 (Boeson 1965) and Feb. 1976 (Veitch 1978). Also recorded Akaroa, Banks Pen. and Hokitika, Westland (Oliver). Stewart I.: two, Halfmoon Bay, 23 Jan. 1956 (CSN 19); single bird, Breaksea Grp, 2 Feb. 1972 (CSN 20). Solander I.: single birds, 9 Dec. 1947 (Falla 1948), 31 Jan. 1973 (Wilson 1973), 25 Nov. 1973 (Nilsson 1974) and 8 Feb. 1984 (Cooper et al. 1986). Chatham Is: single bird (banded as chick Snares Is, Dec. 1971), 21 Feb. 1973 (Robertson 1974). Antipodes I.: single birds, 1 Apr. 1923 and 1 Nov. 1950 (Warham & Bell 1979). Campbell I.: one immature, mid-Feb. 1984 (G.A. Taylor)

MACQUARIE I. Single birds, 1950 (MV: B7312; Simpson & McEvey 1972); 1956–57 (Keith & Hines 1958).

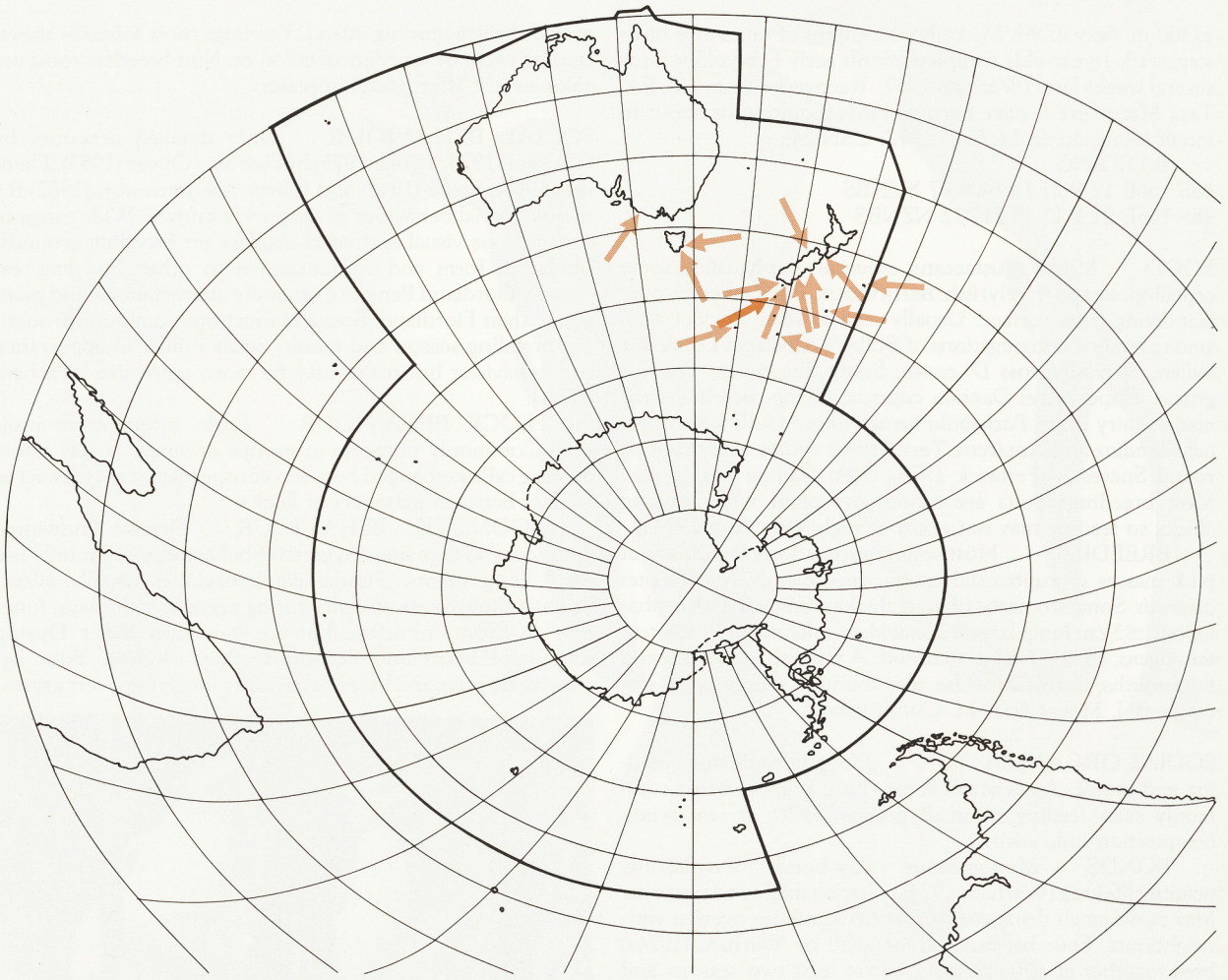
BREEDING During breeding season, mainly met at sea within 5 km of Snares Is, but singles and small groups (<6) up to 80 km from islands (C.M. Miskelly). Only known from four islands in Snares Grp.

Main (North-east) I.: colonies on e. side of island; major concentrations occur at Sinkhole Flat, Penguin Creek, Muttonbird Creek and Hoho Point. In 1968–69, 5000 fledgelings (6204 chicks) (Warham 1974a); in 1986–87, c. 120 colonies, average 160 pairs/colony (1–1900; C.M. Miskelly); 17 600 chicks (SIE 1985–87).

Broughton I.: colonies on e. and ne. (Phoca Bay) sides of island: in 1970–71, 500 chicks (Warham 1974a); 1984–85, c. 26 colonies, average 150 pairs/colony (5–650 pairs) (C.M. Miskelly); 3800 chicks (C.M. Miskelly).

Western Chain: 1983–84, estimated 400–550 chicks: Toru Islet: Feb. 1984, estimated 300–400 chicks; Rima Islet: Feb. 1984, estimated 100–150 chicks (Miskelly 1984).

POPULATION In 1985–86 based on counts of chicks and 73% breeding success per pair (SIE 1985–87), breeding population 23 250 pairs (19 000 on Main I., 3500 on Broughton I. and 750 on Western Chain, where breeding



success 55% per pair) (SIE 1985-87).

Banding data for 5 years gave mean max. mortality in first year 85% and 43% in next 2 years (C.M. Miskelly); estimates of immature population for 1986-87 (based on chick counts from 1982 to 1986) comprised c. 2500 one-year-olds, 2000 two-year-olds, 1000 three-year-olds and lesser numbers of four- and five-year-olds.

Total population (minus chicks) based on above estimates of c. 54 000 birds (A.J.D. Tennyson). Earlier, in 1968-69, total population estimated 30 000-50 000 birds based on counts of chicks on Main and Broughton Is (Warham 1974a). Annual breeding success varies, but mean number of chicks fledging per colony each year apparently increased between 1968-69 (44 fledgelings) and 1986-87 (147) (SIE 1985-87).

Though breeding population confined to small island group, currently under no threat onshore (no introduced predators and landings by people strictly controlled by permit).

MOVEMENTS Dispersive, possibly migratory. Most records of birds away from Snares Is of moulting immatures; not known whether these records reflect post-fledging dispersal.

DEPARTURE Adults leave breeding colonies May, last adult recorded ashore Main I. 30 May (Warham 1974a) but Western Chain breeders probably complete moult in June

(Miskelly 1984). Immatures complete moult and leave earlier than adults, late Jan.-late Mar. Chicks leave breeding areas on Main and Broughton Is early Jan.-mid. Feb., peak 16-22 Jan. (Warham 1967, 1974a); probably not until Mar. from Western Chain where breeding season 6 weeks later (Miskelly 1984).

NON-BREEDING Winter at sea but movements unknown; no evidence yet to support suggestion of northerly migration in winter (Stonehouse 1971).

RETURN Adults arrive breeding colonies 18 Aug. onwards (Horning & Horning 1974). First male seen 20 Aug., with mean arrival date 1 Sept.; first female 30 Aug. with mean arrival date 9 Sept. (Horning & Horning 1974). Banded birds return to same colony and usually to same nest as previous year (Warham 1973, 1974a); of three six-year-olds, one bred at natal colony, two away from it. Some one-year-olds ashore early Nov., with numbers building up until about 20 Jan. (Warham 1974a).

BREEDING Adults leave for pre-moult fattening soon after chicks fledge and main colonies devoid of breeders mid-Feb. to mid-Mar. (Warham 1974a). Return after about 69 days from 17 Mar. onwards; majority back by 26 Mar. (Warham 1974a). Birds banded as chicks return to Snares Is to moult as one- and two-year-olds, mainly above landing points (see Habitat) on coast. Of nineteen three-year-olds, 37% moulted at natal colony, 37% \leq 200 m from natal colony, 26%

≤400 m away (C.M. Miskelly). Moulting of immature birds staggered; 1-year-olds complete moult early Feb., older birds several weeks later (Warham 1967). Recoveries from NZ, SA, Tas., Macquarie I. have been of birds moulting or about to moult (Simpson & McEvey 1972; CSN 24).

BANDING

48S 166E 12 P U 13 1401 67 NZNBS
48S 166E 01 P U 13 217 22 NZNBS

FOOD Mostly crustaceans, especially euphausiids, some cephalopods and (rarely) fish. **BEHAVIOUR.** Food taken by pursuit-diving from surface. Usually seen as small flocks (<20) among feeding congregations of Buller's Albatross *Diomedea bulleri*, Shy Albatross *D. cauta*, Sooty Shearwater *Puffinus griseus*, Cape Petrel *Daption capense*, diving-petrels *Pelecanoides*, Fairy Prion *Pachyptila turtur*, Silver Gulls *Larus novae-hollandiae* and Antarctic Tern *Sterna vittata* over tide-rips round Snares Is (Fenwick 1978). Seen feeding during day. Most breeding adults are ashore overnight while rearing chicks so feeding may not occur at night (Warham 1974a).

BREEDING Most spilt regurgitations at nest are of pink masses of euphausiid crustaceans, mainly *Nyctiphanes australis*. Some stomachs of dead chicks crammed with cephalopods ≤3 cm long; largely *Nototodarus sloanii* and *Moroteuthis ingens*, some *Octopus maorum*. A few fish (<10 cm) and fish otoliths, mainly Moridae, also found in dead chicks' stomachs (P.J. Moors & D.M. Cunningham).

SOCIAL ORGANIZATION Gregarious during breeding and moult. Association at sea, little known. Most commonly seen feeding in small groups (<20) at sea; group composition unknown.

BONDS Monogamous. Pair-bonds long-lasting, possibly lifelong (Warham 1974a). Strong fidelity to nest-site. May move small distances (<2 m) to minimize overlap with neighbours. Four banded pairs studied by Warham (1974a) bred together at same nest-site for at least two seasons and probably more than six seasons because observations 3 and 4 years later showed same pairs at same sites. Divorces not recorded. Changes probably caused by death or absence of partner. Sex ratio unknown. Age at first breeding thought to be 6 or 7 years (Warham 1974a) but data few. Non-breeders commonly pair for short period at end of main breeding season (late Jan.) and perform mock breeding activities (i.e. building, advertising calls, copulation). Not known whether established pairs associate at sea after end of breeding. Both parents incubate, feed and defend young, although not equally at all stages (see Breeding). Chicks form crèches of up to 30 young.

BREEDING DISPERSION Colonial; in medium-sized groups (typically 160 pairs) at densities of up to 2.0 nests/m². Usually nest on open level ground or under *Olearia* and *Brachyglottis* forest. Remain near breeding sites when feeding at sea during mating season (i.e. young are fed daily) but may go further afield during non-breeding season. Nest-site territory only; consists of nest and area within pecking distance; used for courtship, coition, nesting, feeding young, calling out young from crèches and loafing. Defend moulting sites.

ROOSTING On sea during breeding and non-breeding period; breeding birds roost on or near (<2 m) nests during moult; non-breeding birds roost round edges of colonies and with yearlings above landing rocks. Breeding birds commonly roost in small clubs above landing places for short

periods before heading inland. Yearlings roost solitarily above landing rocks or on edges of colonies. Non-breeders roost on colonies just after breeding season.

SOCIAL BEHAVIOUR Only detailed accounts by Warham (1973, 1974a, 1975) but see also Oliver (1953), Fleming (1948), Stead (1948) and Oliver; see Jouventin (1982) for review. Social behaviour at sea poorly known. Wide range of conspicuous visual and vocal displays on breeding grounds; similar in form and circumstances to other *Eudyptes*, especially Fiordland Penguin; generally interact more, and more social, than Fiordland. Social interactions common throughout breeding season and moult. Sexes similar in appearance and behaviour but males may be more aggressive (Warham 1974a).

FLOCK BEHAVIOUR Little information available. Commonly porpoise in groups or singly at sea. Short barking calls exchanged between conspecifics at sea may act as contact between members of flocks.

AGONISTIC BEHAVIOUR Defend individual distances and nest sites. Aggressive behaviours commonly use vocal components. Submissive behaviours usually silent. Bright-yellow crests obvious during aggressive displays; function or effect unknown (but see Jouventin 1982). During submissive behaviour, contour-feathers sleeked. Four aggressive displays and three behaviours involving overt aggres-

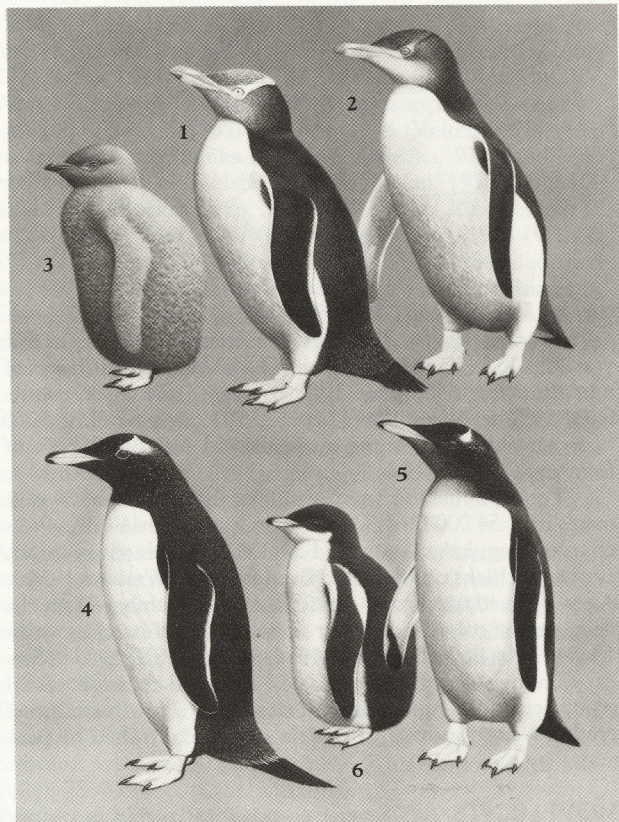


Plate 9

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

sion recorded by Warham (1973, 1974a, 1975). **THREAT.** **Jab-hiss:** bird arches neck, thrusting open bill towards opponent; immediately recoils. Each thrust may be accompanied by brief Hiss. Most common aggressive display. **Forward Gape:** opponents extend necks, bringing widely open gapes nearly into contact; twist heads from side to side as if about to interlock bills; birds may hiss, snort or utter single low-pitched pulsed phrase. Often leads to Bill-lock Twist or Bill-lock Fight. **Forward Trumpeting:** bird raises flippers, leans forward and steps toward opponent, delivering series of loud low-pitched pulsed phrases. **Attack:** bird charges towards opponent with bill open and flippers raised. **FIGHTING.** **Bill-lock Twist:** opponents interlock bills and pull at one another, twisting heads from side to side; performed silently or with single low-pitched pulsed phrase. **Bill-lock Fight:** opponents utter harsh low-pitched pulsed phrases through interlocked bills and swat each other with flipper blows to head and upper body. **Bite-nape Fight:** aggressor bites opponent on nape and swats from behind with flipper blows to sides and back. After fights, winners perform Forward Trumpeting, Vertical Trumpeting, and Vertical Head-swinging. **APPEASEMENT.** Seven submissive displays noted by Warham (1973, 1974a, 1975). **Slender Walk** (Fig. 1): bird walks with head and neck lowered, feathers sleeked, flippers held stiffly forward; often pauses to Stare-around. Most obvious and common form of appeasement. Used when moving through or past defended

nest-sites. Movement especially rapid inside colonies, often involving short hops; also used in clubs above landing rocks. Intensity of display depends on density of nearby territorial birds. **Stare-around:** flippers held forward, bill held upward and to one side, as bird looks obliquely at surrounding owners of territories. **Shoulders-hunched** (Fig. 2): neck lowered, flippers held forward so that shoulder blades protrude, bill pointed downwards; most commonly performed when bird approaches partner for nest-relief. Thought to be primarily submissive. Warham (1973, 1975) suggested possible sexual or recognition function. Slender Walk intergrades with Shoulders-hunched. **Shivering:** flippers, and sometimes head, vibrated rapidly; response to approach or presence of humans (Warham 1973); not known if used between conspecifics. **Bill-hiding:** bird crouches over nest and turns bill away from disturbance; in extreme cases, bill lowered until hidden under body; usually only by females incubating eggs or brooding chicks. **Squeal:** bird utters short high-pitched squeal in response to sudden danger; not associated with any posture. **Flipper Flicks:** bird flicks nearest flipper toward disturbance; flicks both flippers in extreme cases (e.g. in response to aerial predators).

SEXUAL BEHAVIOUR Males establish themselves at breeding grounds before arrival of females. During this time males begin building nest. As more birds arrive, males **ADVERTISE** territorial status and availability to prospective females using **Vertical Head-swinging:** bird points bill upwards, extends flippers and swings head through rapid arcs; utters series of low-pitched pulsed phrases, similar to those used in Trumpeting. Performed most often early in breeding season, especially at dusk or early evening when females tend to arrive, but also commonly throughout breeding season. During **PAIR-FORMATION** and re-establishment of pair-bonds variety of sexual displays performed (Warham 1973, 1974a, 1975). **Mutual Bowing;** members of pair point bills into nest-bowl and utter succession of deep pulsed phrases; frequently leads to Mutual Forward Trumpeting. Occurs before and after laying and during moult. May be performed solitarily and have territorial connotation in some circumstances. **Mutual Forward Trumpet** (Fig. 3): members of pair point bills forward and extend flippers while performing series of long, loud, pulsed phrases; occurs throughout breeding season. Occupant of nest or site will normally exchange Forward Trumpets with returning partner when still some distance from nest; may aid recognition of individuals. Males start performance more often than females. Forward Trumpets often performed solitarily, sometimes used in aggressive circumstances. When used sexually, Mutual Forward Trumpeting often leads to Mutual Vertical Trumpeting. **Mutual Vertical Trumpet:** members of pair face each other, extend flippers and call skyward, using same loud pulsed phrases used in Forward Trumpet; flippers may be raised and lowered in time with call; male usually starts performance. Females sometimes Vertical Head-swing while males Vertical Trumpet. Mutual Vertical Trumpeting occurs throughout breeding season. Solitary birds sometimes Vertical Trumpet round landing rocks, but usually use Vertical Head-swinging instead. Vertical Trumpets may precede or follow Mutual Vertical Head-swinging. **Mutual Vertical Head-swinging:** members of pair bow slightly, swinging heads into nest bowl; utter slow series of pulsed low-pitched phrases; then simultaneously stretch upward, waving heads in wide arcs and giving increasingly rapid series of pulsed phrases. Both sexes use Vertical Head-swinging solitarily, though males more often than females

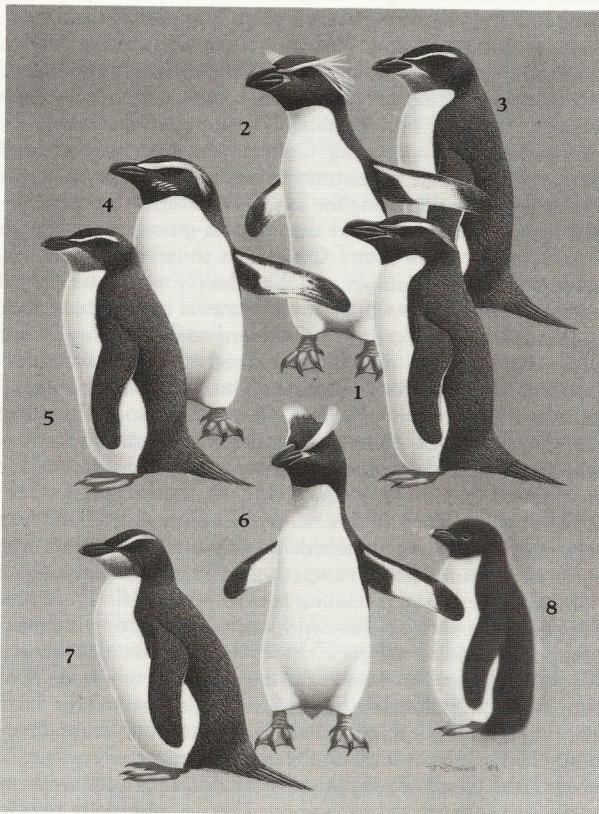


Plate 10
 Snares Penguin *Eudyptes robustus*
 1. Adult
 2. Adult
 3. Juvenile
 4. Adult
 5. Juvenile
 6. Adult
 7. Juvenile
 Fiordland Penguin *Eudyptes pachyrhynchus*
 Erect-crested Penguin *Eudyptes sclateri*
 8. Downy young, mesoptile

Fig. 1 Slender Walk

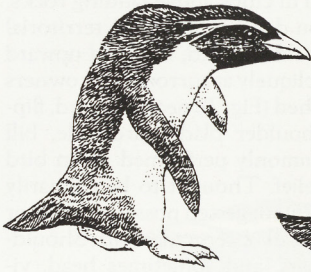
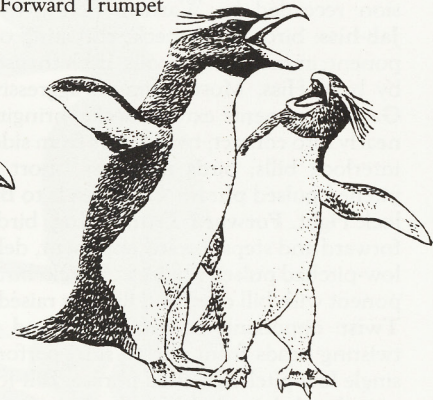
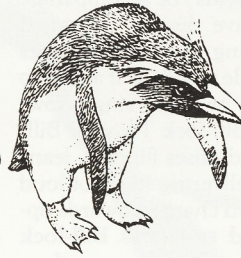


Fig. 2 Shoulders-hunched



Fig. 3 Mutual Forward Trumpet



(Warham 1975). Vertical Head-Swinging has territorial connotations in some circumstances and functions as male advertising display. **Mutual Display:** male performs Vertical Head-swinging as female reaches up to male's head, calling with slightly open bill. Calls similar to those used during Mutual Vertical Head-swinging; performed throughout breeding season by mated pairs but less common than Mutual Vertical Head-swinging. **Quivering:** bird vibrates bill in very small arcs as it bows over nest bowl to deposit nesting material; most commonly performed silently but series of low pulsed phrases similar to those produced during Bowing sometimes used; performed mutually or solitarily. **MUTUAL ALLOPREENING.** Reciprocal or simultaneous; heads, napes, cheeks or throats; common throughout breeding cycle. Warham (1975) suggested that allopreening is first sign that advertising male has accepted female. Not obviously ritualized but mock preens, in which partner's feathers are not touched, sometimes occur. No vocal component. **COPULATION.** Male pats female's back and sides with flippers until she lies prone with flippers held outward. Male then mounts, still patting her sides, and treads on her back while gently billing her nape and head; female raises tail to one side everting cloaca while male lowers his tail to make cloacal contact. After coition, male dismounts and freezes for several seconds, holding bill pressed to one side of upper breast (Warham 1973). Coition most common during week before laying; does not occur after clutch complete. However, first phase of copulatory sequence (i.e. male patting female's back and sides with flippers) common throughout breeding season. Copulation sequences observed in non-breeders, especially after end of breeding season, and between breeders during moult (Warham 1973, 1974a).

RELATIONS WITHIN FAMILY GROUP Males start building nest on arrival at breeding sites. When females arrive 7–8 days later, both collect nesting material but females less often. Nest-bowl also formed primarily by males, using feet and breast in rotating hollowing motion (Warham 1974a). Males present during laying. After laying of second egg, both adults take turns incubating for about 10 days (Warham 1974a). Females take first long incubation stint (c. 12 days) as males go to sea and feed and colonies become quiet. When males take over incubation (c. 12 days) and females go to sea, social interactions become more frequent. At hatching, either male or both parents present. Males stay with chicks throughout guard-stage and preen them regularly. Chicks rest on parents' feet, tucked into brood-patch. Females return daily, usually in early evening, to feed chicks; commonly stay till dawn. Though only females feed young at this stage, chicks beg from either parent. Visits by females set off numerous

Mutual Bowing, Trumpeting and Vertical Head-swinging Displays that appear to be infectious between pairs (Warham 1973). By 18 days old, chicks too large to be brooded and stand next to parent or with only heads tucked under parents. By then, chicks and parents allopreen regularly. During threatening circumstances, chicks push their heads under parent, often begging. By about 3 weeks only one chick usually still alive. Chicks explore regularly at this age and often pick up and carry nesting material. Surviving chicks eventually form crèches, which tend to be in middle of colonies. Crèches commonly disband during evenings as chicks return to nest-sites to be fed. Aggressive behaviour, including adult-like Jabs, aggressive calls, pecks and fights are common in crèches. When attacked by older birds, chicks hunch and attempt to escape by burrowing into centre of crèche. Chicks commonly cheep when in huddles. Chicks in crèche also perform mutual or non-reciprocal allopreening. Crèche formation marks end of guard-stage though males tend to remain on empty nest for 2–3 days before departing for sea. Both parents return at regular intervals to feed chicks during post-guard stage, though females much more often. On return to nest-site from sea, parents Vertical Trumpet and Bow deeply with loud pulsed phrases. If mate present, Mutual Trumpets may occur. Chick responds by leaving crèche and moving toward calling parent with loud begging and flippers raised. Quantitative information on parent/chick recognition little but both have individually distinct types of calls. Chicks can distinguish calls of their parents (I.G. McLean.). Although several chicks may respond to Trumpets of a single parent, only one is fed; others are pecked and driven away, often by the accepted chick. Chicks peck toward adult's bill while begging, inducing it to regurgitate. Arching of female's neck during regurgitation commonly stimulates Trumpeting in nearby males, which may cause her to stop feeding and respond with Trumpets. Begging cheeps are emphasized visually by sharp upward flicks of flippers. Adults will peck chicks that beg too aggressively. Adults regurgitate 6–8 times during course of one feed (Warham 1974a). Chicks place bill inside adult's open bill for 5 to 8 s during each regurgitation. Feeding occurs at or near (<2 m) nest-site. Females still tend to feed young more often than do males toward end of post-guard stage. Crèches may break up somewhat toward end of post-guard stage, especially toward evening when chicks often return to nest-sites and wait arrival of parents. By about 75 days, fully-feathered chicks make their way to sea, often at dawn. Fledging chicks approach sea in twos and threes, turning back frequently. Once in the water, chicks dive but resurface more quickly than adults; then move farther out toward open sea. Adults may depart shortly after

chicks fledge but some remain to perform mock breeding activities (e.g. collecting nesting material, courtship).

VOICE The only quantitative studies of voice are by Warham (1973, 1975). Calls generally persistent, loud, harsh and low-pitched. Most composed of loud discordant pulsed phrase labelled Throb by Warham (1973, 1974a, 1975), used singly or repeated. The only calls that do not fall into this category are Hiss, Bark and perhaps Squeal. Call throughout day, peaking at dusk or early evening; less often later at night. Call consistently throughout breeding season with peaks just after return to colonies, during male- and early pair-phase of egg-stage; less often during moult and at sea. Little quantitative data on sexual differences. Warham (1973, 1975) noted that female's calls higher in frequency than male's, but based on small sample. Variation may be simple consequence of difference in size. Calls of individual birds stereotyped; most variation in length and completeness of calls. Greater variation between individuals (Warham 1973, 1975). General form and quality consistent among conspecifics. Calls similar in form and setting to other crested penguins, especially Fiordland Penguin. Generally lower in pitch with longer phrases than Rockhopper Penguins; higher in pitch with shorter phrase lengths than Erect-crested Penguins. No data on regional variation. Breed only on Snares Islands group, but variation possible between islands.

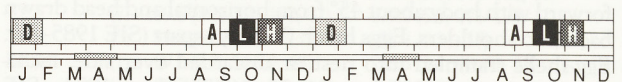
ADULT SEXUAL. Vocalizations associated with **Vertical Head-swinging**: repeated Throb phrases, composed of 20 ms pulses; occasionally begins with brief inspiratory note. Length of Throb, 0.1 s at beginning of display, increasing to 0.25 s midway and ending at 0.3–0.6 s. Throbs separated by 0.14–0.18 s intervals of silence, which increase slightly in length towards end of display. Frequency spanned 0–4 kHz; main energy at 1.0–1.5 kHz and at 2.5–3.5 kHz. Downward slur in pitch toward end of call with shorter pulses and longer intervals of silence. Total length 3.0–6.5 s. Based on sample of 12 males. Amplitude lower than Trumpets. Female calls may be pitched lower (Warham 1973, 1975). Not known whether differences occur between advertising, solo or mutual Vertical Head-swinging. **Bowing**: pitch lower, phrases shorter, intervals of silence longer, and total length shorter than for Vertical Head-swinging or Trumpets. Details not known. Not known if sexual differences occur. No data on variation between mutual or solo performance. **Trumpet**: repeated Throb phrases, each composed of 5–15 60-ms pulses; may include unpulsed, perhaps inspiratory, groan. Length of Throb 0.2 s at beginning of display, increasing to 0.6–0.8 s towards end. Throbs separated by 0.2 s intervals of silence. Frequency spanned 0–4 kHz; main energy at 1–2 kHz. Total length 4.0–5.0 s. Based on sample of 12 males. Female call may be pitched lower (Warham 1973, 1975). No data on variation between forward and vertical Trumpet or between solo or mutual performance. No data on differences between sexual and agonistic Trumpets. **Mutual Display**: repeated, low-pitched Throb phrases, each composed of brief pulses. No details available. See Mutual Display vocalization under Voice in Fiordland Penguin for very similar call. **Quivering**: no details available. Similar to vocal component of Bowing. **AGONISTIC.** **Jab-hiss**: low-pitched, brief (<1 s), not pulsed. Details not known. See Voice in Fiordland Penguin for very similar call. Not known if sexual differences occur. **Forward Gape**, **Bill-lock Twist**, **Fights**: single Throb phrase composed of unpulsed unstructured noise to 4 kHz. Sometimes begins with brief inspiratory note. Length varies greatly, de-

pending on length and type of stimulus; typically 0.2–0.6 s during **Forward Gape**; longer in Fights and Bill-lock Twist. Frequency spans 0.2–4.0 kHz; main energy at 1.0–1.5 kHz but varies. Based on sample of six males. Not known if sexual differences occur. **Forward Trumpets**. See Trumpet under Sexual vocal behaviour. **Squeal**: low-pitched, not pulsed. Details not known (see Squeal under Voice of Fiordland Penguin). **OTHER CALLS.** **Contact Call**: short, simple, low-pitched pure note. Details not known (see Contact Call under Voice of Fiordland Penguin). **NON-VOCAL SOUNDS.** During fights, sound of flippers rapidly bashing against opponent, loud and striking. Flipper-patting of females by males during copulation also obvious but not so loud. Various sneezing, coughing and snorting sounds associated with comfort. Snorts sometimes given during aggressive display, Forward Gape. Sometimes produce snoring sound while sleeping (Warham 1973).

YOUNG Chicks beg using simple cheeps lasting 0.14–0.30 s and repeated at 0.5–0.7 s intervals. Pitched at 3.0–5.0 kHz; much higher than adult calls. In example given by Warham (1973, 1975), each cheep characterized by brief rise and fall in pitch followed by longer and more pronounced rise and fall. Call rate increases as chick sights parent. Calls of particular chick very constant in form and patterning; greater variation between chicks. Begging cheeps given throughout development. At later stages of development and in post-guard stage, calls become more varied. Harsh noisy cries, more highly pitched than adult calls, given during aggressive actions and fights.

BREEDING Well known. Field studies by Warham (1973, 1974a), Snares Is Expedition 1985–87 (SIE 1985–87), Stonehouse (1971) and others. Based on contribution by C.M. Miskelly and J.O. Waas. Breeds in small to medium-sized monospecific colonies (means c. 160, max. 1900 pairs); only on Snares Is where in 1968–69 population was 30 000–50 000 birds in 133 colonies; more recent estimate of 54 000 birds in 1986–87 (A.J.D. Tennyson). Nest under forest or scrub or in swampy or rocky areas.

SEASON Colonies occupied from late Aug. to early Feb. Main I: first eggs 18 Sept. (Horning & Horning 1974), latest 19–20 Oct. (Warham 1974a); Western Chain: laying probably about 6 weeks later in mid-Nov. (Miskelly 1984). Males arrive from 18 Aug. (mean arrival 1 Sept.) and defend nest-sites; females arrive from 30 Aug. (mean arrival 9 Sept.) (Horning & Horning 1974). Both sexes stay till 5–26 days after laying when male goes to sea (Warham 1974a). Adults leave colonies mid Jan.–early Feb., return to moult late Mar. Chicks leave Main I, 2 Jan.–14 Feb., with peak departure 16–22 Jan. (Miskelly 1984; SIE 1985–87); Western Chain, departure probably not till early Mar. (Miskelly 1984).



(Main I.)

SITE On ground. Colonies in flat muddy areas under forest or in open; also on rock ledges and platforms; usually sheltered by *Olearia*, *Brachyglottis* trees, *Hebe* scrub or rock falls, screens; sometimes exposed. Colonies usually conspicuous, noisy; even under forest because there is little ground cover. Sites generally stable from year to year with

pairs returning to same nest but some colonies move, change shape or are abandoned as vegetation is killed. Other species rarely enter colonies; single Rockhopper Penguins (twice in three seasons) and one Fiordland Penguin noted defending empty nests in colonies (C.M. Miskelly). Maximum density of nests: 2/m²; bases of nests 35.7 cm (9.6; 21–58; 25) apart (Warham 1974a).

NEST, MATERIALS Shallow cup, sometimes raised on platform; of twigs, small branches, vegetable matter and mud (Warham 1974a); on Western Chain, of granite chips, fish and bird bones because there is little soil or vegetation. Mostly built by male (Warham 1974a), collecting material within or near colony; carrying it in bill and depositing it on rim of nest with rapid quivering motion. Birds scrape out hollow by lying across area and scooping out soil with their feet as they rotate (Warham 1974a). Mean diameter of nest: 27.8 cm (2.1; 25; Warham 1974a).

EGGS Short oval to almost oval, short sub-elliptical or pyriform (Warham 1974a); mat, chalky; pale blue-grey when fresh, soon becoming stained. A-egg averages 27.5% less in volume than B-egg (SIE 1985–87).

MEASUREMENTS.:

A-egg: 67.1 (2.6; 62.4–71.4; 23) x 51.1 (1.7; 47.2–53.9);

B-egg: 72.1 (2.5; 68.5–79.4; 23) x 56.0 (1.2; 52.8–59.5) (intact clutches; Warham 1974a).

WEIGHTS.:

A-egg: 90.0 g (6.3; 10);

B-egg, 117.0 g (6.0; 10) (fully-incubated unpipped eggs; SIE 1985–87).

CLUTCH-SIZE Two, but in colony of 43 pairs in 1985, 1 x C/1, 42 x C/2 (SIE 1985–87); more than C/2 unknown.

LAYING Synchronized; in one colony, all eggs laid 21 Sept.–20 Oct. 1972, half having A-egg by 28 Sept. and half having both eggs by 2 Oct. (Warham 1974a); Western Chain, mean date of laying about 12 Nov. (Miskelly 1984). No information on annual variation. Interval between A- and B-eggs: 4.4 days (4–5; 66) (Warham 1974a; SIE 1985–87). Eggs laid at any time of day or night. No replacement if egg lost. Single-brooded.

INCUBATION Incubation starts with B-egg but A-egg guarded continuously. Both sexes stay at nest for few days after clutch complete, changing over often (Warham 1974a). Male leaves after 10 days (2.9; 5–16; 24), having been ashore for 37.3 days (5.6; 23–46; 32); almost all males gone by 15 Oct. 1972. Females then sit for 12.1 days (3.4; 9–25; 36) till relief by male, having been ashore for 39.0 days (4.4; 33–55; 15) (Warham 1974a); about half females relieved by 26 Oct. 1972; almost all by 31 Oct. Males then incubate till hatching and stay during guard-stage. During incubation, eggs held in brood patch (under flap of loose skin) 3–4 cm wide on lower abdomen with B-egg nearer feet and A-egg in front; adult leans forward with body about 45° from horizontal and head drawn back into shoulders. Eggs hatch 0–4 days apart (SIE 1985–87). Egg-shells trampled into nest or discarded over side. **INCUBATION PERIOD.:** 33.4 days (31–37; 46) (Warham 1974a; SIE 1985–87). Birds will sit on addled eggs for 3–4 weeks beyond period (Stead 1948; Warham 1974a).

NESTLING Semi-altricial, semi-nidicolous. Protopile, dark brown above, white below; bill, blackish with horn-coloured tip. Mesoptile acquired in 9–12 days (SIE 1985–87), medium chocolate-brown above, pale buff below. Down shed from about 24 Dec., first from abdomen, leading-edge of flippers, then lower back, belly chin; last on base of flippers,

crown, nape; some chicks almost down-free by 2 Jan., most not till 12–16 Jan. (Warham 1974a). **NESTLING PERIOD.:** no quantified data but about 75 days. Brooded and guarded continuously by male; probably fed about daily by female during guard-stage; female does not feed male and goes to sea between feeding visits. Usually only one chick survives guard-stage. Adults defend nest-bowl against all intruders. Crèches form towards end Nov. at age about 3 weeks, when male goes to sea after about 33 days ashore; crèches usually contain fewer than 30 chicks (6–12 typical), change size and place often but mostly in centre of colony in between brooding birds and other adults (Warham 1974a). Both sexes feed chicks during crèche-stage but female most. Fed by incomplete regurgitation, chicks placing bill inside that of parents; food not retrieved if spilt on ground; no feeding between adults (Warham 1974a).

GROWTH Poorly known. Mean weight at fledging: 2.53 kg (0.21; 1.85–3.0; 50) (Stonehouse 1971); 2.66 kg (0.23; 2.15–3.20; 120) (Warham 1974a); i.e. c. 86% of mean adult weight. Measurements at fledging: bill, 47.7 mm (2.5; 43–54; 50); flipper, 179 mm (5; 172–193; 50); foot, 111.6 mm (4.4; 103–122; 50) (Stonehouse 1971).

FLEDGING TO MATURITY Young usually leave in early morning, reach launching rocks soon after dawn; no evidence for adults conducting young thither and chicks often attacked en route if they approach an adult. No data on behaviour, relation with adults, etc. after departure. Little knowledge of later life: one 4-year-old seen with partner and chick once; youngest known breeder, 6 years old; two other 6-year-olds and one 7-year-old found with eggs or chicks and probably breeding (Warham 1974a).

SUCCESS At two colonies (SIE 1985–87): 430 pairs built nests; 375 (87.2%) laid two eggs each; 349 (93% of layers) hatched at least one chick; 275 chicks fledged (no twins); thus, 73.3% of laying pairs reared a chick or c. 64% of total population were successful or 37% of all eggs laid produced fledgeling. At most closely studied colony (43 nests): 84 eggs laid, 68 (80%) hatched, 35 chicks (51.5%) fledged for total success of 41.2%; or 81.4% of breeding pairs fledged a chick. Only one substantiated example of twins being reared, out of 1049 active nests (SIE 1985–87), but one adult in each of six separate colonies has been seen to feed two chicks (SIE 1985–87). Of 305xC/2, about 64% hatched both eggs but one chick usually died of starvation before 10 days old (4.7; 193) (Warham 1974a; SIE 1985–87). Banding returns: on average 15% of fledgelings survive for a year; 57% survivorship in following two years (C.M. Miskelly). No further information. Oldest known bird 18+ years. **PREDATORS.** Adults occasionally taken by Hooker's Sea Lions *Phocarctos hookeri* and Leopard Seals *Hydrurga leptonyx* (Warham 1974a; Horning & Fenwick 1978; SIE 1985–87). Fledgelings killed by giant-petrels *Macronectes* spp near shore and at launching rocks. Skuas *Catharacta* sp, only potential predators on land; not recorded taking chicks but middens near colonies regularly have egg-shells and carcasses of chicks; not thought to affect productivity greatly (Warham 1974a). Other causes of mortality not known but many chicks may die in exposed colonies during bad weather (Warham 1974a). No harvesting of penguins known and human activity probably not a menace. Leech *Ornithobdella edentula*, commonly found at edge of colonies, feeds on adults and chicks.

PLUMAGES

ADULT In fresh plumage: **HEAD AND NECK.** Crown

to lower neck, sides of neck and head and inter-ramal space to lower throat, dark black-brown (119). Some filoplumes on cheeks. Tips of chin-feathers, slight, brown (119B). Light grey-brown (119D) bases of cheek feathers sometimes exposed during breeding and throat display, forming parallel stripes as in Fiordland Penguin (Warham 1974a,b). Long straw yellow (57) superciliary stripe, silky in texture, extends from groove of latericorn and ramicorn to hindcrown; narrow at anterior end, widening posteriorly. Varies in width; narrower in females than males (Warham 1974b). At hindcrown, superciliary stripe develops into crest, 50 mm long; feathers parted, drooping, splayed laterally; intermixed with long dark black-brown (119) feathers at outer margin of crown (Stonehouse 1971; Warham 1974a). Feathers of hindcrown longer than on crown. **UPPERPARTS.** Mantle, back, rump and upper tail-coverts, dark black-brown (119); tips, light blue-grey (88); prominent near flanks and at rump. In worn plumage, during pre-moult, dorsum, dark brown (119A). **TAIL.** Rectrices, short, rigid at base, black-brown (119); tips, light blue-grey (88); prone to wear. **UPPERFLIPPER:** feathers, scale-like anteriorly, longer posteriorly, ordered in distinct rows; dark black-brown (119); tips, light blue-grey (88); prominent at base and posteriorly. Two posterior rows of feathers on flipper, white, from carpal flexure to near tip. **UNDERPARTS,** white; demarcation at lower throat, convex; slight inward progression of white feathers at lower neck, extending as straight line to side of thighs. Feathers of underparts longer than in Fiordland Penguin; see Stonehouse (1971) for details. **UNDERFLIPPER,** white with dark black-brown (119) patches near axilla and tip; patch near axilla extends narrowly along anterior margin. Individuals vary in extent of axillary patch towards tip and in extent of blackish suffusion at tip; variation not related to sex (illustration in Warham 1974a). Concealed bases of feathers, light grey-brown (119D) at base merging to dark brown (119A); black-brown (119) at tip.

DOWNY YOUNG Protoptile, down short; head, hindneck, sides of neck and upperparts, dark brown (219); from lower throat, rest of neck and underparts, dull white. Upper surface of flipper, as dorsum; lower surface, similar to underparts. Mesoptile, thicker; head, including throat, and upperparts, dark brown (119A). Underparts, white. Upper surface of flipper, as dorsum; lower surface, similar to underparts.

JUVENILE Juvenile plumage retained until 15 months old; indistinguishable from adult after post-juvenile moult (Warham 1974a). **HEAD AND NECK.** Crown to nape, and auricular area, dark black-brown (119). Chin, throat, malar region and cheeks, light grey-brown (119D); feathers short; tips, dark brown (119A). Superciliary stripe, narrow, cream (54); feathers short. Crest much reduced; almost white before moult (Warham 1974a). Hindneck and sides of neck, similar to crown. Lower throat to base of neck, white. **UPPERPARTS,** similar to adult. Larger light blue-grey (88) tips to feathers impart bluer cast. **TAIL, UPPERFLIPPER,** similar to adult, but blue colour more marked. **UNDERPARTS,** similar to adult.

ABERRANT PLUMAGES Melanistic and partial melanistic birds recorded (Warham 1974a).

BARE PARTS Based on photos in Lindsey (1986) and at NZDOC library.

ADULT Iris, rufous (41); in some birds, pinkish-red or claret (Warham 1974a). Bill, rufous (140). Bare skin round base of bill, dull pink (5); extends round base of latericorn and ramicorn; fleshy. Rictus, triangular, pink (7). Front of tarsus,

toes and webs, dull pink (5) to pink (7). Distal edge of webs, hind tarsus and soles, dull dark-brown (219). Claws, grey-black (82).

DOWNY YOUNG Iris, dark brown (121). Bill, black-brown (119); tips of upper and lower mandibles, cream (92). Rictus and bare skin round base of bill, reduced, grey-black (82). Front of tarsus, toes and webs, pale pink-white. Rest like adult; dark brown (219) on webs more extensive.

JUVENILE Similar to adult; iris lighter, dark brown (219A).

MOULTS Based on Warham (1974a), except where stated.

ADULT POST-BREEDING In adult breeders: birds at sea for c. 69 days before returning to natal colony to moult, c. 17 Mar. Moult at nesting site. Complete; rectrices shed first; duration 24–30 days; late Mar.– early May. Most complete by 20 Apr. Presumed non-breeders return late Jan.; moult early Feb.–mid Mar., on edges of colony. Straggler in s. Aust. beginning moult 8 Jan. (Simpson & McEvey 1972).

NATAL Complete; mesoptile first shed c. 24 Dec.; almost gone by 2–16 Jan.; lost last from base of flippers, crown and nape.

POST-JUVENILE Yearlings return mid–late Nov.–Dec. Complete; first moult 5 Jan., 50% in moult 20 Jan.; depart c. 8 Feb.; in captivity, duration c. 22 days. Growth of tail, body feathers and crest continues after departure. After this moult, indistinguishable from adult; occurs at c. 15 months old. Details of subsequent moults of known-age birds (non-breeders) in Warham (1974a).

MEASUREMENTS (1) Breeding adults (Jan., Feb.), live; methods described (Stonehouse 1971). Warham (1974a) notes that sample may have included non-breeders. (2) Breeding adults, live; methods described (Warham 1974a). (3) Yearlings; methods described (Warham 1974a). (4) Breeding adults, live; methods described (Warham 1974a). (5) Breeding adults, live; methods described (Warham 1974b). (6) Main I., paired breeders (9–10 Jan. 1985); methods undescrbed (C.M. Miskelly). (7) Toru Islet, Western Chain, paired breeders (29 Dec. 1984); methods undescrbed (C.M. Miskelly).

(B)= bill measurements at base, (G) = bill measurements at gonys.

	MALES	FEMALES	
FLIPPER	(1) 183.0 (4.2; 170–193; 61)	177.3 (3.9; 167–187; 47)	**
	(2) 183.0 (4.49; 6)	176.7 (3.18; 6)	
	(3) 180.8 (3.9; 47)	174.6 (4.2; 48)	
	(4) 183.2 (4.9; 35)	178.5 (3.25; 5)	
	(5) 184.0 (5.1; 114)	178.8 (4.1; 82)	
	(6) 189.0 (3.8; 181–195; 20)	180.0 (3.7; 170–186; 20)	
	(7) 189.0 (5.0; 175–197; 17)	179.0 (5.5; 171–194; 17)	
TAIL	(5) 93.9 (5.87; 42)	92.4 (6.21; 37)	
BILL	(1) 59.2 (2.2; 54–69; 68)	52.5 (2.1; 49–61; 58)	**
	(2) 58.7 (2.90; 6)	52.0 (1.83; 6)	
	(3) 55.0 (2.2; 54)	49.9 (2.3; 53)	
	(4) 59.1 (2.47; 35)	52.3 (1.60; 5)	
	(6) 58.6 (2.2; 54.7–62.7; 20)	52.5 (1.9; 49–56.2; 20)	
	(7) 56.8 (1.8; 53.7–60.1; 17)	50.6 (1.8; 47.5–54.6; 17)	
	BILL D(G)	(2) 27.7 (1.57; 6)	24.2 (1.13; 6)
	(3) 23.0 (1.1; 54)	20.8 (1.1; 53)	
	(4) 28.2 (1.13; 35)	24.5 (2.06; 5)	
BILL D(B)	(6) 33.7 (1.3; 31.5–36; 20)	29.5 (1.2; 27.8–32.5; 20)	
	(7) 33.3 (1.7; 30–36.4; 17)	28.8 (1.3; 25.2–30.6; 17)	

BILL W(G)	(1)	12.8 (0.61; 11.5-14.3; 64)	11.1 (0.58; 9.6-12.2; 54)	**
	(2)	12.5 (0.65; 6)	10.6 (0.45; 6)	
	(3)	11.0 (0.6; 54)	9.8 (0.5; 54)	
	(4)	12.5 (0.57; 35)	10.6 (0.51; 5)	
BILL W(B)	(6)	28.4 (1.4; 26.9-32; 20)	25.6 (1.6; 22.8-28.3; 20)	
	(7)	28.8 (1.7; 25.1-32.1; 17)	25.7 (1.5; 23.8-28.7; 17)	**
FOOT	(1)	115.3 (3.7; 108-127; 58)	108.4 (4.4; 99-114; 41)	**
	(2)	114.0 (3.75; 6)	109.0 (2.60; 6)	
	(5)	114.4 (3.7; 12)	109.0 (2.6; 12)	
TOE	(5)	78.4 (2.3; 42)	73.7 (6.0; 43)	**

(8) Snares Is, assumed yearlings, live; methods described (Stonehouse 1971). (9) Skins; methods described (Stonehouse 1971).

UNSEXED				
FLIPPER	(8)	178.0 (5.2; 162-189; 61)		
	(9)	160.3 (0.93; 141-180; 14)		
BILL	(8)	52.9 (3.1; 45-59; 75)		
	(9)	54.9 (0.40; 47-61; 16)		
BILL W(G)	(8)	11.0 (0.72; 9.7-12.8; 75)		
FOOT	(8)	113.5 (4.48; 100-122; 61)		
	(9)	105.8 (0.61; 92-115; 15)		

Adult proportions are reached in yearlings, except in bill; adult size of bill probably achieved in both sexes during third or fourth years (Stonehouse 1971). For measurements of newly-fledged chicks see Stonehouse (1971).

WEIGHTS Weights in kg. (1) Adults, live (Stonehouse 1971). (2) Breeding pairs (Nov.), live (Warham 1974a). (3) Breeding pairs (Jan.), live (Warham 1974a). (4) Yearlings (pre-moult), live (Warham 1974a). (5) Yearlings (Nov.) (Warham 1974a).

MALES		FEMALES	
(1)	3.32 (0.347; 2.45-4.30; 41)	2.78 (0.300; 2.30-3.40; 32)	
(2)	2.630 (0.222; 6)	2.484 (0.137; 6)	
(3)	3.361 (0.282; 6)	2.700 (0.155; 6)	
(4)	4.340 (0.311; 30)	3.876 (0.441; 23)	
(5)	2.873 (0.216; 24)	2.647 (0.206; 39)	

Fledging weights given in Warham (1974a) indicate sexual dimorphism in weight from early age.

(6) Yearlings, live (Stonehouse 1971).

UNSEXED

(6) 3.66 (0.706; 2.30-5.20; 75)

Weights vary with sex, age and season; heaviest in pre-moult. Weight loss occurs during incubation; in females, pronounced in Nov.; in males, pronounced during guard-stage, when attending chicks. In Jan., both sexes feeding large chicks. During moult, loss of weight linear. Few data for adults. Yearlings lose 47% initial weight; 100-105 g/day; mean weights of unsexed yearlings, pre-moult: 4159 (425; 52); in moult: 2050 (240; 87). See Warham (1974a) for details.

STRUCTURE Flightless. Flipper long, broad at base, bony and hard. Feathering of body dense, strongly lanceolate; rachis broad and flattened at tips; imparts glossy appearance. Tail, short; wedge-shaped; c. 14 rectrices, t1 longest; prone to wear. Ventral surface of rachis on rectrices, concave. Bill, robust; hooked at tip; fits into groove on mandibular unguis (Stonehouse 1967; illustration in Warham 1975). Culminicorn bi-convex, parallel-sided when viewed from above. At base of culminicorn, arcuate ridges (growth lines) and parallel median striations, latter extending forwards. Legs very short, feet webbed. Pads of soles thick. Claws, long and curved. Outer toe c. 88% of middle, inner c. 64%, hind c. 17%. Both sexes have brood patches during incubation (details in Warham 1974a).

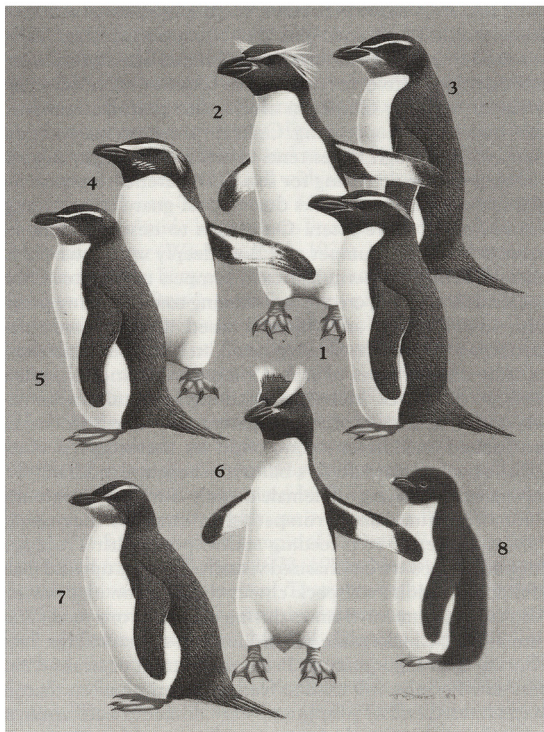
SEXING, AGEING Sexually dimorphic in bill size; males larger. Bill shape index (bill-length x bill-width x bill-depth [mm]/10, see Warham [1972] for details): adults: males >1780, 2036 (220; 6); females <1550, 1332 (113; 6). Toe lengths in adults and differences in behaviour used for sexing (Stonehouse 1971; Warham 1974a). Age-classes distinguished on plumage and other criteria (Warham (1974a).

GEOGRAPHICAL VARIATION Forms superspecies with *E. pachyrhynchus* and *E. sclateri* (Peters). Monotypic; see Geographical Variation section of *E. pachyrhynchus* for reasons for retaining specific status. Population on Western Chain possibly reproductively isolated; breeds 6 weeks later than other populations (C.M. Miskelly).

RMO

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Volume 1 (Part A), Plate 10

Snares Penguin *Eudyptes robustus*

- 1. Adult
- 2. Adult
- 3. Juvenile
- 8. Downy young, mesoptile

Fiordland Penguin *Eudyptes pachyrhynchus*

- 4. Adult
- 5. Juvenile

Erect-crested Penguin *Eudyptes sclateri*

- 6. Adult
- 7. Juvenile

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