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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

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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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Eudyptes sclateri Erect-crested Penguin

Eudyptes sclateri Buller, 1888, Birds NZ, ed.2, 2: 289 - Auckland Islands.

Named in honour of P.L. Sclater, FRS (1829-1913), Sec. Zool. Soc. London.

OTHER ENGLISH NAMES Big-crested, Sclater's or (in error) Macaroni Penguin.

Erect-crested refers to the diagnostic erectile feathers of the superciliary crests, compared with the somewhat drooping crests of other crested penguins.

MONOTYPIC

FIELD IDENTIFICATION Length 67 cm; flipper 195-225 mm; bill 50-60 mm; weight: male 4.9 kg, female 4.1 kg. Moderately large penguin, large for genus, with slim brownish-orange bill; bright-yellow superciliary stripe starts near gape and rises obliquely over eye, forming brush-like, erectile crest. Bare whitish skin at base of bill. Head has domed profile and characteristic 'large-chinned' appearance when seen from side. Sexes alike but male larger than female with noticeably larger bill when seen together. No seasonal changes. Juveniles and immatures separable.

DESCRIPTION ADULT. Head, rich velvet-black with conspicuous broad pale golden-yellow superciliary stripe, starting near gape and rising obliquely over eye to form long brush-like erectile crest of silky feathers up to 6 cm long. Some birds have thin line of yellow feathers running from superciliary stripe parallel with bill towards nostril. Viewed from front, superciliary stripes are more or less parallel. Cheek-feathers, jet-black. Viewed from side has dome-shaped head and characteristic large chin, extending towards tip of bill. Flippers long, blue-black dorsally with thin white trailing edge of 2-3 rows of white feathers. Dorsal plumage and long tail, bluish black. Sharp demarcation across throat separates black face from silky white abdomen. Underflipper, whitish boldly marked with black, with large black patch at tip joined to body by thick black leading-edge, and black patch at posterior base. Bill, long and slim, brownish orange. Culminicorn usually with parallel sides and straight ridge. Bluish-white skin separates base of mandible from feathers and forms prominent triangle at gape. Eye, brown. Feet and legs, pink above but blackish brown behind tarsi, soles and front of webs. Claws, brown. Before moult (Feb.), head becomes brown, superciliary stripes fade, and dorsal plumage has bronze cast. Immediately after moult (Apr.), dorsal feathers are shiny with strong bluish cast. At sea, look for brownish bill, whitish skin at base of bill, black cheeks, and broad superciliary stripe starting near gape and rising obliquely over eye. Crests flatten against side of nape when wet. FLEDGELING. Smaller than adult. Superciliary stripe yellow, projecting 1 cm from back of head. Chin, dirty white with same characteristic shape as adult. Dull-white feathers on cheeks and throat. Dorsal plumage, shiny dark blue. Underside of flipper as boldly marked as adult. Bill smaller than adult's and dull black with 1-cm palehorn tip. No bare skin at base of bill but fleshy triangle visible at gape. Eye, dark brown. Feet and claws, as adult. ONE-YEAR-OLD. Smaller than adult. Superciliary stripe broad, whitish to pale yellow; crests short and not erect. Superciliary stripes appear parallel when viewed from front. Chin grey, sometimes whitish. Dorsal plumage, brown-black. Bill, slender,

dull brown-orange, sometimes with trace of pale tip. Bare skin round gape and along base of mandible not conspicuous. Before moult (Jan.), yearling appears scruffy about head, with whitish superciliary stripe and brownish dorsal plumage. Most stragglers are of this age group. After moult, yearlings have velvet-black faces and short yellow crests that are erect posteriorly. Underflipper as adult. Birds of the year difficult to identify at sea, but look for clearly defined broad superciliary stripe that starts near gape and rises obliquely over eye. TWO-YEAR-OLD. As adult but with shorter crests.

SIMILAR SPECIES Most similar to Snares Penguin E. robustus but resembles all other crested penguins. ADULT. Snares, shorter, with stouter, more orange bill with bulbous culminicorn. Superciliary stripe thinner, brighter yellow and starts near nostril before passing back horizontally over eve. Crests droop more, posteriorly. Superciliary stripes diverge in V from bill when seen from front. Viewed from side has flatter crown and smaller chin than Erect-crested. Markings on underflipper less distinct. Fiordland E. pachyrhynchus, shorter and dumpier, with shorter stouter orange bill with bulbous culminicorn. No bare skin at base of bill. Superciliary stripe starts near nostril and passes back horizontally over eve to form drooping crest. Superciliary stripes diverge in V from bill when viewed from front. Dark cheeks typically have several white stripes radiating out from base of bill. Less domed crown and smaller chin than Erect-crested; markings on underflipper less distinct. Rockhopper E. chrysocome, with which Erect-crested shares several breeding islands, much smaller, with smaller orange bill. Bare skin at base of bill less prominent or absent. Eye, bright red. Superciliary stripe very thin, starting 1-2 cm back from nostril and passing horizontally over eye to form long fibrous drooping crest. Crest includes more black feathers, and joined across crown by black occipital crest. Macaroni E. chrysolophus and Royal E. schlegeli, taller, with longer, more massive orange 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. JUV-ENILE, ONE-YEAR-OLD. Snares, shorter, more compact, with bill more orange and bulbous. Narrow superciliary stripe more yellow and starts near nostril to pass horizontally over eye. Superciliary stripes form diverging V from bill. Chin smaller and usually darker. Markings on underflipper less distinct. Fiordland, shorter and dumpier, with short bulbous orange-brown bill that lacks fleshy margins. Broad whitish superciliary stripe starts near nostril and passes horizontally over eye. Superciliary stripes form diverging V from bill. Chin smaller, markings on underflipper less distinct. Rockhopper,

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much smaller, with small orange bill and thin, poorly developed superciliary stripe that starts 1-2 cm from naricorn before passing horizontally over eye. Eye redder, and black occipital crest already noticeable. Macaroni and Royal, taller, with longer, more orange bills and bright-pink triangle of skin at gape. No superciliary stripe but messy patch of chrome-yellow and white feathers on forehead.

Breed in large colonies on Bounty and Antipodes Is and in smaller numbers at Campbell and Auckland Is. Absent from breeding places from May to early Sept. but movements at sea unknown. Usually walk on land, but hop when hurried. Swim with head and part of back above water; porpoise when swimming fast. Vagrants solitary, often among other crested penguins. Voice deeper, more musical, and call delivered more slowly than Snares, Fiordland and Rockhopper Penguins.

HABITAT Marine in subantarctic and cool temperate waters round NZ, especially round Bounty and Antipodes Is. Breeding adults thought to forage close to subantarctic breeding islands, because chicks fed frequently (J. Warham). Assumed to be pelagic outside breeding season but winter distribution poorly known; regular records in NZ, Feb.-Sept., suggest use of warmer waters off e. coast of SI after breeding.

Breed on three subantarctic island groups S of NZ; also formerly Campbell I. Nest in rocky terrain, tolerating small islands without land vegetation or substantial soil; on boulder beaches, rocky flats, slopes and ledges, and among rock falls (Westerskov 1960; Bailey & Sorensen 1962; Bell 1975; Warham & Bell 1979; Robertson & van Tets 1982). Attempted breeding on NZ mainland, Otago Pen., under *Hebe* scrub on steep slope 200 m from sea (Richdale 1941). On Antipodes I., nest from just above high water to 75 m asl (Warham & Bell 1979); Bounty Is, from spray zone almost to summits of islands at 70 m asl.

Breeding birds moult at nest-sites (Richdale 1941, 1950; Warham 1972); immatures, at colonies or along rocky coasts elsewhere. Diving depths unknown.

DISTRIBUTION AND POPULATION Two main islands of NZ and offshore islands; vagrant to Macquarie I., Chatham Is and s. Aust. Recorded Falkland Is, Nov. 1961– Jan. 1967 (Napier 1968; Wood 1975). Breed Bounty, Anti-



podes and Auckland Is; formerly Campbell I.

at sea during breeding season: 160 km ESE of Bounty Is, 2 Dec. 1773; heard, 150 miles E of Bounty Is, 15 Nov. 1774 (Beaglehole 1961); several groups on approach to Bounty Is, 12 Jan. 1968 (Darby 1970). Records of beachcast and live birds in NZ during moult (Feb.-Apr.), mainly on e. coast of SI; probably largely immatures, as most breeders moult at nestsites. After completion of moult in late Apr.-early May birds leave breeding islands and spend next 4 months at sea. Winter records in Cook Str. and on e. coast of SI suggest northward movement from breeding islands in winter, with some birds reaching coastal waters off e. coast of SI (Falla 1935, 1942; Powlesland 1984).

AUST. Vic. Specimens: MV Reg. No. B249, Lady Julia Percy I., about 1 Aug. 1891 (Learmonth 1952); MV Reg. No. B6383, Carrum, 15 Feb. 1954 (Hitchcock 1956). Live bird, moulting, Phillip I., 22 Feb. 1979 (Brown 1983). Tas. One, beachcast, Trefoil I., 5 Feb. 1983 (Tas. Bird Rep. 1984), SA. Granite I., 21 Mar. 1965 (Hutchins & Parker 1976). WA. Esperance, Mar. 1972 (Serventy & Whittell 1976).

Before 1955, records from NI (North C., Castle-NZ. cliff, n. side Cook Str.) and SI (White I., C. Campbell, New Brighton, Birdlings Flat, Timaru) (Oliver). Since about 1960, small numbers reported nearly every year, mainly in moulting period, Feb.-early May: three times in NI (Whangarei Heads. C. Turnagain, Taranaki) but mostly in SI, particularly along Canterbury and Otago coasts, occasionally in Southland and Stewart I. Recorded less often in winter, mainly from Cook Str. and along e. coast of SI. Rare (two records) Oct.-Jan. (CSN; Notornis Reps Beachcast Birds; NZ Atlas).

CAMPBELL IS Reported annually in fair numbers up to 200.

SNARES IS Reported annually (c. 30/year).

CHATHAMIS Vagrant: Mar. 1979, 1 Feb. 1954, 10 Jan. 1984 (Dawson 1955; Veitch 1981; Oliver; C.M. Miskelly).

MACQUARIE I. Vagrant; mainly in moulting period (Oliver; Keith & Hines 1958; Warham 1969; Aust. CL).

NZ only: Antipodes and Bounty Is in BREEDING large numbers; Auckland I. (Disappointment I.) in small numbers; formerly Campbell I.; attempted breeding Otago Pen. (NZCL; Richdale 1941, 1950). One bird attempted to breed with a Rockhopper Penguin at Devil's Nose Rookery, Westpoint I., Falkland Is in 1964-65 and 1965-66 (Napier 1968).

Antipodes Is. Total population probably similar to Bounty Is (P.J. Moors); round coast of Main I. (Warham & Bell 1979); largest colonies along ne. and sw. coasts and opposite Orde Lees Islet (P.J. Moors); Bollons I., Archway I. (Warham & Bell 1979).

Auckland Is. Disappointment I.: only one pair found 1972-73 but likely to breed elsewhere among Rockhopper Penguins (Bell 1975).

Bounty Is. 1978: estimated 115,000 pairs on Spider, Depot, Proclamation, Tunnel, Penguin, Ruatara, Lion, Funnel Is, Mooy Cap (Robertson & van Tets 1982).

Campbell I. No recent breeding records; 1986-87: c. 20-30 pairs but no eggs or chicks (P.J. Moors). Formerly: below Mt Azimuth, Oct. 1945, c. 170 birds; Yvon Villarceau: Jan. 1945, small colony; Dec. 1945, 20 birds; Oct 1946: 15 nests; and probably elsewhere (Bailey & Sorensen 1962).

POPULATION Total population between 100 000 and 1 000 000 pairs (J. Warham); probably about 200 000 breeding pairs mostly confined to Bounty and Antipodes Is.

Other than Campbell I., population, distribution and num-Pelagic distribution poorly known. Few records of birds bers appear stable. Breeding habitat essentially unchanged and under no threat at present. No recognized influence by humans. Rats may prey on eggs and chicks (Robertson & Bell 1984).

> **MOVEMENTS** Dispersive, possibly migratory, but distribution in winter poorly known (see Distribution). Most records of birds away from breeding areas are of moulting immatures; not known whether these records reflect postfledging dispersal.

> Adults probably leave Antipodes Is DEPARTURE mid-Apr., but Bounty I. breeders probably later (J. Waas; C. Miskelly) where breeding season 3 weeks later (Robertson & van Tets 1982). Immatures complete moult and leave earlier than adults, in mid-Mar. (Warham 1972). Chicks leave breeding areas, Antipodes I., mid-Jan. to mid-Feb., peak 30 Jan. (Warham 1972).

> NON-BREEDING Winter at sea, possibly regularly including waters off e. coast of SI, N to Cook Str. (Powlesland 1984; see Distribution).

> RETURN Adults return to breeding colonies early Sept. (Warham 1972).

> BREEDING Adults leave for pre-moult fattening soon after chicks depart. On Antipodes I., main colonies devoid of breeders by 4 Feb.; return after about 4 weeks, from 21 Feb. onwards; most back by 9 Mar. (Warham 1972). On Otago Pen., one female absent for 40 days (Richdale 1957). Immatures return mid-Mar. (Warham 1972).

> FOOD Reported as crustaceans and cephalopods (J. Warham); no other information.

> SOCIAL ORGANIZATION Gregarious during breeding and moult. Size and composition of groups at sea unknown, but Robertson & van Tets (1982) observed flocks (50-300) close offshore.

> BONDS Monogamous. No detailed data on duration of pair-bonds or fidelity to nest-site; a pair retained same nest site for 2 years before male disappeared; female returned to same site for 7 years (Richdale 1941). No data on divorce. Sex ratio unknown. Age at first pairing unknown. Not known whether established pairs associate at sea outside breeding season. Both parents incubate, feed and defend young. Chicks form crèches.

> BREEDING DISPERSION Colonial; in large groups (>1000 pairs). Distance between centres of nests approximately 66 cm (n=20; Warham 1972). Densities on Bounty I., 1 nest/1.4 m² in mixed colonies with Shy Albatross and 1 nest/0.8 m² in pure colonies (Robertson & van Tets 1982). Usually nest on open, level or gently sloping ground. often in mixed colonies with Rockhopper Penguins or Shy Albatross Diomedea cauta. Dispersion at sea unknown but probably feed near nesting sites during breeding season. Nestsite territory only; consists of nest and area within pecking distance; used for courtship, coition, nesting, feeding young. calling young from crèches and loafing. Defend moulting sites.

> ROOSTING Details not known. Breeding birds roost on or near nest-sites during moult; non-breeders roost within or near colonies after breeding season and during moult. Breeding birds and non-breeders commonly rest in

small clubs above landing places for short periods before moving to colonies.

SOCIAL BEHAVIOUR Only accounts by Warham (1972, 1973, 1975) and Richdale (1941, 1950, 1951); review by Jouventin (1982). Warham's account incomplete as field work was conducted for only 6 weeks at end of breeding cycle. Richdale studied a single pair nesting on Otago Pen.; breeding unsuccessful and probably atypical. Social behaviour at sea poorly known. Employ wide range of conspicuous visual and vocal displays on breeding grounds. Social repertoire similar in form and circumstances to other Eudyptes spp, especially Fiordland and Snares Penguins. Generally less aggressive toward conspecifics and humans than other crested penguins. Social interactions common during breeding season and moult. Sexes are similar in appearance and behaviour but Warham (1972) suggested that males were more aggressive.

FLOCK BEHAVIOUR Little information. Porpoising noted (Robertson & van Tets 1982); short barking calls exchanged between conspecifics at sea may be contact calls between members of flock (Voice).

AGONISTIC BEHAVIOUR Defend individual distances and nest sites. Aggressive behaviours commonly with vocal components; submissive behaviours usually silent. Bright-yellow crests obvious during agonistic displays. Unique among crested penguins in ability to raise and lower crests; function or effect not known. During submissive behaviour contour-feathers are sleeked. AGGRESSIVE BE-HAVIOUR. Six aggressive displays and three behaviours involving overt aggression recorded (Warham 1972, 1973, 1975). THREAT. Point-growl. Bird points slightly open bill toward opponent and produces low pitched growl (Voice); low-intensity aggressive behaviour; performed by both sexes. Jabvell(/hiss). Bird arches neck, thrusts open bill toward opponent and immediately recoils; each thrust may be accompanied by brief sharp yell (Warham 1972; Voice) or hiss (Warham 1973; Voice). Side-look Gape. Bird tilts head to one side with one eye fixed on opponent; freezes with gape wide open; performed silently. Forward Gape. Opponents extend necks, bring wide open gapes into near contact; twist heads from side to side as if preparing to interlock bills; each may perform single low-pitched yell (Voice). Often leads to Billlock Twist or Bill-lock Fight. Forward-trumpeting. Bird raises flippers, leans forward and steps towards opponent delivering series of loud low-pitched pulsed phrases (Voice). Attack. Bird charges toward opponent with bill open and flippers raised. FIGHTING. Bill-lock Twist: opponents interlock bills and pull at one another while twisting heads from side to side; performed silently or with single low-pitched yell (Voice). Bill-lock Fight. Opponents utter coarse low-pitched yells (Voice) 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. Post-aggressive Display. Birds commonly stand erect following performance of aggressive displays and drop bills down to upper breast (Warham 1972), similar to behaviour of males following copulation. Winners may also perform Forward-trumpeting, Verticaltrumpeting, and Vertical Head-swinging. APPEASEMENT. Five arcs 20-40° from vertical and utter an increasingly rapid series submissive displays or attitudes noted (Warham 1972, 1973, of pulsed phrases (Voice); flippers held back and separated by 1975). Bill Hiding. Submissive behaviour performed by con- only 30-40°. Both sexes perform solitarily though males more geners (see Snares and Fiordland Penguins) not observed but often (Warham 1972, 1975). Vertical Head-swinging most no observations made when display is typically performed. common display but less infectious than Trumpeting displays; Slender Walk. Bird walks with neck and head lowered, feath- sometimes has territorial connotations and also functions as

ers sleeked, flippers held stiffly forward and crests flat against head; often pauses to Stare-around. Most obvious and common form of appeasement; performed when moving through or past defended nest-sites; movement especially rapid inside colonies. Intensity of attitude depends on proximity of defending birds. Stare-around. Bird holds flippers forward and bill upward and to one side, and looks obliquely at owners of surrounding territories, often jerking head from side to side. Shoulders-hunched. Neck lowered and flippers held forward so that shoulder blades protrude; head and bill turned slightly to one side. Most common when bird approaches partner for nest-relief; thought to be primarily submissive. Warham (1972, 1973, 1975) suggested possible sexual or recognition functions. A female studied by Warham (1972) adopted this posture when avoiding attempts to copulate by her partner. Performed by both sexes (Warham 1972). Slender Walk intergrades with Shoulders-hunched. Squeal. Short high-pitched squeal (not associated with any posture) in response to sudden danger (Voice). Flipper Flicks. Bird flicks nearest flipper toward disturbance; in extreme cases (e.g. in response to aerial predators) flicks both flippers.

SEXUAL BEHAVIOUR ADVERTISING. Vertical Head-swinging. Bird directs bill upward, extends flippers and swings head in slow wide arcs; utters series of low-pitched pulsed phrases similar to Trumpeting (Voice). Males advertise territorial status and availability to prospective mates; performed during breeding season and moult. During PAIR-FORMATION and re-establishment of pair-bonds, variety of sexual displays performed (Warham 1972, 1973, 1975). Mutual-bowing. Paired birds point bills into nest-bowl and utter series of deep pulsed phrases (Voice). Females start this more often than males; performed during breeding season and moult. Bowing also performed solitarily and may have territorial function. Frequently leads to Mutual-trumpeting or Mutual Display. Mutual Forward-trumpet. Paired birds point bills forward with crests flat against head and flippers out-stretched; utter series of long loud pulsed phrases (Voice). Occurs during breeding season and moult; most common form of Trumpeting. Occupant of nest normally Forwardtrumpets when returning partner still some distance away; may aid pair-recognition. Males start this more often than females. Forward-trumpets frequently performed solitarily and sometimes used in aggressive circumstances. Highly infectious between conspecifics during breeding season and moult. In sexual encounters often leads to Mutual Vertical-trumpeting. Mutual Vertical-trumpet. Paired birds face each other, extend flippers and vocalize skyward using pulsed phrases louder than those used in Forward-trumpet (Voice); crests flat against head; flippers may be raised and lowered in time with calls. Male usually starts this; females sometimes Vertical Head-swing while male Vertical-trumpets. Occurs during breeding season and moult; highly infectious between conspecifics. Rarely performed by solitary birds, which use Vertical Head-swinging. Vertical-trumpets may precede Mutual Vertical Head-swinging. Mutual Vertical Head-swinging. Members of pair bow slightly swinging heads into nest-bowl as they utter slow series of pulsed low-pitched phrases; birds simultaneously stretch upward, wave heads slowly in wide

male advertising display. Mutual Display. Male performs Vertical Head-swinging as female reaches up to male's head. calling with slightly open bill; female's flippers held to sides. Vocalizations similar to those used during Mutual Vertical Head-swinging (Voice). Performed throughout breeding season by mated pairs but less common than Mutual Vertical Head-swinging. Highly infectious among breeding birds. Quivering. Bird vibrates slightly open bill in very narrow arcs as it bows over nest-bowl to deposit nesting material; may rotate in nest during display or turn bowed head from side to side. Most commonly performed silently; by both sexes but most often by females. MUTUAL ALLOPREENING. Reciprocal or simultaneous; heads, napes, or necks; no vocal component. Common throughout breeding cycle; suggested that this is first sign that advertising male has accepted female (Warham 1975). Not obviously ritualized. COPULATION. Male pats back and sides of female with flippers till she lies prone with flippers held outward and bill slightly raised; male then mounts, still patting her sides and treads on her back while gently billing cheeks and side of nape; female raises tail to one side everting cloaca as male lowers tail to make cloacal contact. After coition, male dismounts and freezes for several seconds holding bill pressed to one side of upper breast (Warham 1972, 1973). Most commonly preceded by Trumpeting and Bowing displays. Most common during week before laying in other crested penguins but no observations from this period available (but see Richdale 1941). Copulation by breeders and non-breeders observed before and during moult (Warham 1972).

RELATIONS WITHIN FAMILY GROUP Estimated arrival at breeding colonies mid-Sept. (Warham 1972); suggestion that males may arrive before females as in other crested penguins but no observations conducted during this time (Warham 1972). Both partners collect nesting material but females less often. Nest-bowl formed using feet and breast in rotating hollowing motion, possibly more often by males (Warham 1972). Both adults incubate but no reliable details on lengths of incubation shifts or contribution by sexes (Warham 1972). No observations of guard-stage or feeding of hatchlings. Chick rests on parent's feet, tucked into brood patch. When too large to brood stands next to parent; chicks and parents allopreen regularly. During threatening situations, chicks push heads beneath parent, often begging. Chicks explore regularly and often pick up and carry nesting material. Surviving chicks eventually form crèches, which tend to be in middle of colonies. Aggressive behaviour, including adult-like Jabs, aggressive calls (Voice), pecks and fights are common between chicks in crèches. Also perform mutual or non-reciprocal preening. Formation of crèches marks end of guard-stage. Both parents return to feed chicks during post-guard stage though females more often (Warham 1972). On return to nest-site from sea, parent Forward-trumpets; if mate present, Mutual-trumpets may occur. Chick responds by leaving crèche, moving toward calling parent with loud begging calls and flippers raised. Feeding chase usually follows. Quantitative information on parent/chick recognition little but both possess individually distinct types of calls. Although several chicks may respond to Trumpets of a single parent, only one is fed. Chicks peck toward adult's bill while begging, inducing regurgitation. During regurgitation, adult arches its back and erects crest. Begging cheeps (Voice) are emphasised visually by sharp upward flicks of flippers; adults peck mildly at chicks apparently when they beg too aggressively, especially when feeding completed. Adults regurgitate 6–10 times during course of feed (Warham 1972). Chick's bill placed inside adult's open bill for short periods during each regurgitation. Feeding does not necessarily occur near nest-site. Females still tend to feed young more often than males late in the post-guard stage. When fully feathered, chicks make way to sea. Adults depart shortly after.

VOICE The only quantitative studies of voice by Warham (1973, 1975). Generally, calls are persistent, loud, and low-pitched; most composed of loud discordant pulsed phrase labelled Throb by Warham (1972, 1973, 1975). Calls that do not fall into this category are Hiss, Yell, Bark, Growl and perhaps Squeal. Call throughout day to early evening; less often later at night. No details on seasonal variation. Lower levels of calling during moult and at sea. Little quantitative data available on sexual differences. Female calls higher in frequency but based on small sample (Warham 1973, 1975), Variation may be simple consequence of difference in size. Calls of an individual stereotyped with less variation than between individuals. Most variation within individuals in length and completeness of calls (Warham 1973, 1975). General form and quality consistent among conspecifics. Calls similar in form and setting to other crested penguins, especially to Fiordland and Snares Penguins. Generally much lower in pitch and more sonorous than these species, with Throbs delivered at more measured rate. No data on regional variation. Variation between island groups is likely.

ADULT SEXUAL. Vocalizations associated with Vertical Head-swinging; repeated throbs, each composed of 60-ms pulses overlaid by bands of sound which fall in pitch at end of each phrase. Occasionally begins with brief inspiratory note. Length of throb 0.15 s at beginning of displays, increasing to 0.4–0.5 s toward end. Throbs are separated by fairly constant 0.1-0.2-s intervals of silence. Frequency spanned 0-3.5 kHz but main energy at 1.0-1.5 kHz and at 1.5-2.5 kHz. Total length 3.0-6.0 s. Based on sample of five males. Amplitude lower than Trumpets. Female displays may be lower in pitch (Warham 1973, 1975). Not known whether differences occur between advertising, solo or mutual Vertical Head-swinging performances. Bowing. Details not known. Total length shorter, pitch lower, phrases shorter and intervals of silence between phrases longer than Vertical Head-swinging vocalizations or Trumpets. Not known whether sexual differences occur. No data available on variation between mutual or solo Bowing performances. Trumpet. Repeated throbs, each composed of 6 to 12 50 to 60-ms pulses with decrease of pitch towards end. May have brief unpulsed inspiratory groan before each pulse. Length of throb 0.5 s at beginning of display, increasing to 0.9-1.7 s toward end. Throbs separated by 0.2-s intervals of silence at beginning of display, increasing to 0.3 or 0.4 s toward end. Frequency spanned 0-3.8 kHz but main energy at 1.5-2.0 kHz. Total length 4.0-14.0 s. Based on sample of 13 males. Female call may be lower pitched (Warham 1973, 1975). No data available on variation between forward and vertical Trumpet or on variation during solo or mutual performance. No data available on differences between Trumpets given in sexual or agonistic situations. Mutual Display. No details available. Repeated, low-pitched throb phrases, each throb composed of brief pulses (see Mutual Display under Voice in Fiordland Penguin for very similar call). AGONISTIC. Pointgrowl. No details provided by Warham (1972, 1973, 1975). Very low-pitched series of short pulses. Jab-yell (Hiss), Forward Gape, Bill-lock Twist and Fight. Single vell

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phrase. Not pulsed. Harnonics clear and constant. Often starts and ends with groan. Duration varies much and depends on length and type of stimulus. Typically 0.5 s long during Jab-yell or Forwarc Gape but ranges from 0.4 to 0.9 s. Longer in Fights and Bill-lock Twist. Frequency spans 0.5-3.0 kHz with main energy at 1.0-1.5 kHz, but varies. Note that hiss (see Hiss under Voice of Fiordland Penguin for very similar vocalization) may replace yell during some performances of Jab behaviour. Hiss is unpulsed, low in pitch and brief (<1 s). Not known if sexual differences in form of yell or hiss occur. Forward-trumpets. See Trumpet under Sexual vocal behaviour. Squeal. Low-pitched; not pulsed; details not known (see Squeal under Voice of Fiordland Penguin for very similar vocalization). OTHER CALLS. Contact Call: short, simple pure note; low-pitched (see Contact Call under Voice of Fiordland Penguin). NON-VOCAL SOUNDS. During fights, sound of flippers rapidly bashing against opponent loud. Flipper patting of females by males during copulation not so loud. Various sneezing, coughing and snorting sounds associated with comfort movements.

YOUNG Chicks beg, using simple cheeps lasting 0.14–0.30 s and repeated at 0.5–0.7-s intervals. Pitched much more highly than adult calls (i.e. 3.0–6.0 kHz). In example given by Warham (1973, 1975) each cheep characterized by very brief rise and much longer, sharp fall in pitch. Rate of call increases when parent sighted. Calls very constant in form and patterning. Greater variation between chicks in structure of calls. At later stages of development and in post-guard stage, calls become more varied. Harsh noisy cries, higher in pitch than adult calls, given during aggressive interactions and fights. However, simple cheep begging calls performed throughout development.

BREEDING Contributed by J.O. Waas and C.M. Miskelly. Field studies by Richdale (1941, 1951, 1957) and Warham (1972); no detailed studies during pre-laying, incubation and early nestling periods. Breed in large (1000s) colonies, monospecific or among Shy Albatrosses or near Rockhopper Penguins; on rocky flats, at base of cliffs, or above boulder beaches.

SEASON Colonies occupied from early Sept. to late Apr. On Antipodes I., first birds arrive about 5 Sept. and probably stay at nests till laying; first eggs, 2 Oct.; main laying period early to late Oct., peak at 12 Oct. (Warham 1972; see also Richdale 1941). On Bounty Is apparently 2–3 weeks later; eggs, 7–10 days incubated, on 7 Nov. (Robertson & van Tets 1982). Mean date of hatching variously estimated at about 17 Nov. (Warham 1972; Moors 1980; Robertson & van Tets 1982; B.D. Bell). On Antipodes I. adults leave late Jan. to early Feb. but return to moult late Feb. to early Mar.; chicks leave late Jan. to mid-Feb, peak about 30 Jan.

H	D	1	-			-	-	A	L		F		D	-		-		-	-	A	1		-
J	F	M	A	M	J	J	A	S	0	N	D	J	F	M	A	М	J	J	A	S	0	N	D

SITE On ground; on boulder beaches, rocky slopes; some sites protected by boulders, overhangs, in caves; very conspicuous. Sites probably used year after year by same birds (Richdale 1950). On Antipodes I. generally on fairly flat, open ground, often between boulders; in open areas closely packed, centres of nests av. 66 cm apart (46–91; 20; Warham 1972). On Bounty Is in monospecific colonies $(1 \text{ nest}/0.8 \text{ m}^2)$ on lower slopes; among Shy Albatross in flatter areas and higher gullies $(1 \text{ nest}/1.4 \text{ m}^2; \text{ Robertson & van Tets 1982}).$

NEST, MATERIALS Shallow hollow, rimmed with small stones, sometimes grass, and guano where out of reach of rain and spray (Warham 1972); at Bounty Is, with loose accumulation of mud and debris, which tends to be washed away by rain (Robertson & van Tets 1982); at Campbell I., with small pebbles, no vegetable matter (Bailey & Sorensen 1962).

EGGS Blunt ovoid; chalky; pale bluish (Oliver), slightly tinged palish green (Richdale 1941), becoming stained brownish.

MEASUREMENTS:

A-Egg: 76.8 (6.6; 88.5-71.7; 5) x 48.1 (2.2; 46.0-50.0);

B-Egg: 88.8 (2.1; 92.5-87.0; 6) x 56.9 (1.4; 58.2-54.5).

WEIGHTS:

A-Egg: 98 g (90-117; 4);

B-Egg: 149 g (133-170; 4) (Richdale 1950).

Other measurements and weights by Bailey & Sorensen (1962), Oliver from Antipodes, Bounty and Campbell Is are worthless because A- and B-eggs were not identified.

CLUTCH-SIZE Two (Richdale 1950; Oliver). Aegg normally discarded (Robertson & van Tets 1982) and, if replaced, again discarded within 24 h (Richdale 1941).

LAYING No details of synchronization. Interval of at least 48 h between eggs (Richdale 1941). No further data; none on replacement after loss.

INCUBATION Richdale (1941) noted continued incubation for over one month after expected hatching at about 35 days. Attendance and share by sexes uncertain; on 17 inspections in afternoon by Richdale (1941), during 22 days after laying of B-egg, female was sitting each time, male was present for 14, but this pair was nesting in isolation. Method of incubation like that of Rockhopper Penguin (Oliver). Richdale (1941) noted that one end of egg was on ground but most of it was held on adult's toes, which turned inwards so that egg could not roll forward; adult sat with body at 45° angle with egg hidden in brood patch (pouch) or fully prostrate over nest. Incubating birds accepted onions, apples and oranges as substitutes for eggs (Robertson & van Tets 1982). INCUBATION PERIOD: not recorded. No further information.

NESTLING Semi-altricial, semi-nidicolous. Downy when hatched; smoky brown on head, throat and upperparts, white below; bill blackish with light tip; feet blackish (Oliver; age of chick not given). No detailed knowledge of parental care. Chick fed mostly by female towards end of nestling period; by incomplete regurgitation; 6–10 feeds in one bout while chick chased adult; often fed away from nest (Warham 1972). Adults defend eggs and chick vigorously against skuas Catharacta sp at Antipodes I. (Moors 1980).

GROWTH No information. Measurements and weights of chicks, sexed by lengths of bill (Warham 1972), within 2 days of fledging: males: weight, 3.63 kg (0.2; 45; 74% of adult male weight); bill, 50.6 mm (3.1; 38); flipper, 208 mm (5; 58); females: weight, 3.0 kg (0.22; 56; 73% of adult female weight); bill, 48.3 mm (2.8; 56); flipper, 197 mm (4; 40).

FLEDGING TO MATURITY No information on behaviour of chicks at departure, associations at sea; nor on age of pairing, first breeding, longevity.

SUCCESS No information. PREDATORS. Skuas take many eggs and chicks at Antipodes I. (Moors 1980). Northern Giant-Petrels *Macronectes halli* gather at colonies during time of fledging; eat dead birds but not seen to kill (Warham & Bell

1979). Breeding islands uninhabited and rarely visited; human interference improbable.

PLUMAGES

ADULT In fresh plumage: HEAD AND NECK, Crown to lower neck, sides of neck and head, and interramal space to lower throat, dark black-brown (119). Long straw yellow (57) superciliary stripe, silky in texture, extends from top of rictus; narrow at anterior end, widening posteriorly. At hindcrown, feathers longer and more parted; erect and splayed laterally, forming crest; feathers intermixed with long dark blackishbrown (119) feathers at outer margin of crown; crest feathers up to c. 60 mm long. When wet, feathers flattened against head; birds can raise and lower crests when displaying (Richdale 1941; Warham 1972). Newly moulted birds, often nonbreeders, have most upright crests; breeders have longer crests that droop towards rear (Warham 1972). UPPERPARTS. Mantle, back, rump and upper tail-coverts, black brown (119); tips of feathers, 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, blackbrown (119); tips, light blue-grey (88); prone to wear. UPPER-FLIPPER. Feathers scale-like anteriorly, longer posteriorly, ordered in distinct rows. Dorsal surface, dark black-brown (119); tips light blue-grey (88); prominent at base and posteriorly. Two posterior rows of feathers, white, extending from carpal flexure to near tip; narrow white anterior margin. UNDERPARTS. Entire underparts from lower throat, including neck, white; demarcation at lower throat, convex (triangular; Warham 1972); slight inward progression of white feathers at lower neck and mid-flanks, extending as straight line to thighs. UNDER-FLIPPER, white; black-brown (119) patch at posterior base, extending along anterior margin to near tip. At tip, similar dark patch. Concealed bases of feathers, light greybrown (119D) merging to dark brown (119A); dark blackbrown (119) near tip.

DOWNY YOUNG Protoptile, short, silky: head, hindneck, sides of neck, and upperparts, dark brown (219); rest of neck and underparts from lower throat, dull white. Flipper: upper surface, similar to upperparts; lower surface, similar to underparts. Mesoptile, thicker; head, including throat, and upperparts, dark brown (119A). Underparts, white. Flipper: upper surface similar to upperparts; lower surface similar to underparts.

JUVENILE Penguins (q.v.).

ABERRANT PLUMAGES Entire and partial melanistic, and partial albinistic birds recorded (Falla 1935; Richdale 1941; Oliver).

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

ADULT Iris, dark red-brown (132). Bill, red-brown (132A to 132B). Rictus, triangular, pink (7) or pink-white; bluish white (Warham 1972). Rictus and bare skin round base of bill, fleshy, extends round base of latericorn and ramicorn, dull white with pink shade. Front of tarsus, toes and webs, pink (7). Distal edge of webs, hind tarsus and soles, dull darkbrown (219). Claws, grey-black (82).

DOWNY YOUNG Iris, dark brown (121). Bill, black-brown (119); tips of upper and lower mandible, cream (92) for 10-15 mm; assumed when mesoptile lost (Warham 1972). Rictus and bare skin round base of bill, reduced, greyblack (82).

IUVENILE Iris, dark brown (223). Bill, red-brown (132B). Rictus, pink (7); reduced. Rictus and bare skin round base of bill, similar but very narrow. Rest similar to adult.

Based on Warham (1972), except where MOULTS stated.

ADULT POST-BREEDING At Antipodes I., fatten at sea before moult, return to natal colony and moult at nest-site; of adult breeders, most first arrivals are males. Moult complete; Mar.-Apr.; 50% of birds shed feathers early Mar.; last feathers moulted are rectrices; duration c. 26-30 days; mean departure date 3 Apr. Failed breeders later than breeders; departure 11-14 Apr. (Richdale 1941). Duration of moult for adult non-breeders, 26-28 days, from 1 Feb.-6 Mar. (Warham 1972). Stragglers at Macquarie I. moult at about same period (Warham 1969).

POST-IUVENILE At natal colony. Complete: Jan.-Feb.; depart early Feb., some as late as early Mar.; duration unknown, sequence unknown. After this moult, indistinguishable from adult.

MEASUREMENTS (1) Antipodes I., paired breeders before moult, live; methods described (Warham 1972). (2) Antipodes I., moulted yearlings, live; methods described (Warham 1972). (3) Antipodes I., chicks about to fledge, live; methods described (Warham 1972). (G) = bill measurements at gonys.

		MALES	FEMALES	101.00
FLIPPER	(1)	212.0 (6.6; 44)	204.0 (4.6: 44)	**
	(2)	208.0 (6.1; 33)	198.0 (5.4; 46)	
	(3)	208.0 (4.5; 58)	197.0 (3.5; 40)	**
BILL	(1)	58.5 (1.94; 44)	52.5 (1.88; 44)	**
	(2)	57.7 (1.9; 36)	51.8 (2.0; 48)	
	(3)	50.6 (3.1; 38)	48.3 (2.8; 56)	**
BILL D(G)	(1)	26.0 (1.2; 44)	22.6 (1.2; 44)	**
	(2)	22.9 (0.8; 37)	20.6 (1.0; 48)	
	(3)	18.7 (1.0; 38)	17.8 (1.1; 56)	**
BILL W(G)	(1)	12.2 (0.61; 44)	10.5 (0.60; 44)	**
	(2)	11.1 (0.5; 37)	9.7 (0.4; 48)	
	(3)	9.1 (0.6; 38)	8.6 (0.5; 56)	**

See Warham (1972) for additional measurements of 126 Similar to juvenile Fiordland and Snares unsexed adults (status unknown) before moult, and for discussion of growth in age classes.

> **WEIGHTS** (1) Antipodes I., paired breeders before moult; methods described (Warham 1972). (2) Antipodes I., presumed successful breeders; methods described (Warham 1972). (3) Antipodes I., moulted yearlings; methods described (Warham 1972)

	MALES	FEMALES				
(1)	6382 (520; 22)	5434 (431: 22)	**			
(2)	6556 (414; 8)	5522 (439; 9)				
(3)	3368 (350; 31)	2847 (280; 46)				

Weights vary with sex, age and season; heaviest in premoult. In adult non-breeders, 50% of initial weight lost during moult; males 20% heavier throughout than females. Mean weight of adult male non-breeders at start of moult, 7005 (647; 9); at end of moult, 3578 (93; 9). In females, mean weight at start of moult, 5850 (366; 6); at end of moult, 2940 (139; 6). Weight loss is linear. Possible that non-breeders are heavier than breeders in early stages of moult (Warham 1972).

STRUCTURE Flightless. Flipper hard and bony, long relative to body, broad at base. Feathering of body dense, strongly lanceolate; rachis broad and flattened at tips; imparts glossy appearance. Tail, short; wedge-shaped; 14 rectrices, t1 longest, t7 80 mm shorter; prone to wear. Ventral surface of rachis on rectrices concave. Bill robust, hooked at tip; fits into groove on mandibular unguis. Culminicorn parallel-sided, though occasionally absent; evident also in chicks (Warham 1972). At base of culminicorn, arcuate ridges (growth lines) and parallel median striations, latter extending forwards. Crown rather domed (Warham 1972). Legs very short, feet webbed. Pads of soles thick. Claws, long and curved. Outer toe *c.* 92% of middle, inner *c.* 66%, hind *c.* 20%.

SEXING, AGEING Sexually dimorphic in bill measurements; males larger. Bill-shape index (bill-length x bill-width x bill-depth [mm]/ 10, see Warham [1972] for details): adults: males >1600, mean index 1864 (191; 22); females <1400, 1257 (139; 22). Similarly, yearlings: males >1300, 1435 (90; 38); females <1200, 1060 (130; 57). Age-classes distinguishable on plumage; behavioural criteria also used (Warham 1972).

RECOGNITION Adults differ from NZ congeners in having superciliary stripe originating from top of rictus, lower than in *E. pachyrhynchus* and *E. robustus*; crest erect, no part reaches below eye. Eyes and bill, browner lacking reddish shade; feathering of head, darker; rictus and bare skin round base of bill, paler than in *E. robustus*; tail and flippers, long relative to body (Warham 1972). For summary of distinguishing characteristics see Falla (1935), Warham (1972, 1975), Oliver (1953) and Oliver.

GEOGRAPHICAL VARIATION Forms superspecies with E. pachyrynchus and E. robustus (Peters). 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 pachyrlnynchus* 4. Adult 5. Juvenile

Erect-crested Penguin *Eudyptes sclateri* 6. Adult 7. Juvenile

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