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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 schlegeli Royal Penguin

Eudyptes schlegeli Finsch, 1876, Trans. NZ Inst. S: 204 - Macquarie Island.

Named in honour of Prof. H. Schlegel, 1804-88, Director of Leiden Museum.

MONOTYPIC

FIELD IDENTIFICATION Length 65–75 cm; flipper 225 mm; bill 52–75 mm; weight 5–6 kg. Medium-sized to large penguin with massive red-brown bill. Larger than other *Eudyptes* penguins, except very similar Macaroni Penguin *E. chrysolophus*. Black above, white below; diagnostic white or pale grey cheeks and throat, and orange-yellow plumes that rise from forehead and project back or dangle on either side of face. Sexes alike but separable when pairs seen together; males larger than females with markedly larger bill. No seasonal plumages but before moult (Feb.-Apr.) dorsal plumage becomes brownish. Immatures and juveniles recognizable.

DESCRIPTION ADULT MALE. Crown black with very conspicuous long chrome-yellow, orange and black plumes rising from central orange-yellow patch on forehead. Plumes project backwards along crown or droop behind eye. Yellow feathers separated from bill by 1 cm of black feathers. Cheeks from crest to throat, pure white to pale grey (very rarely dark grey or black). Band of grey often separates white cheeks from white underbody in palest birds. Flippers, blueblack dorsally with thin white trailing-edge. Dorsal plumage and tail, slaty black with steely blue sheen. Usually small patch of white on rump. Underflipper dark at tip and posterior base; blackish strip extends for varying distance along leading-edge from base. Bill, huge, dark, orange-brown with bulbous culminicorn. Base of culminicorn on old birds often has transverse series of ridges and grooves. Bare skin round base of bill forms prominent deep-pink triangle at gape. Eye reddishbrown. Legs and long slender feet, bright pink but blackish on back of tarsi and on soles. Claws, dark brown. Before moult (Mar.), dorsal feathers become dull bronze; immediately after moult (Apr.), grey-blue. ADULT FEMALE. As male but slightly smaller with bill shorter and less robust. Cheeks and throat, often uniformly pale grey, rarely as white as in male. At sea, crests flatten against head but look for pale face, large orange bill and orange-vellow patch on forehead. FLEDGELING. Smaller than adult. Head plumes composed of scattered small yellow feathers on forehead. Chin and throat, light to dark grey. Dorsal plumage, dark blue. Bill much shorter and less robust than adult's, blackish-brown. Eye, dull brown. Feet and claws as adult. ONE-YEAR-OLD. Smaller and slimmer than adult. Head plumes very short, often appearing as dense mat of yellow and white feathers on forehead with wispy strands behind eye. Cheeks and throat tend to be greyish rather than white. No white patch on rump. Bill smaller and slimmer than adult, chocolate-brown, lacks ridges on culmen. Bare skin at gape, bright pink. Eye, dull brown to bright red-brown. Before moult (Jan.-Feb.), yearlings appear brown on back. After moulting yearlings are small and slim with short bright orange-yellow head plumes, pale-grey cheeks and throat, and shiny blue-black dorsal plumage. Bill, small, dull brown. TWO-YEAR-OLD. As adult but smaller with shorter crest.

SIMILAR SPECIES Very similar to Macaroni Penguin, which differs in having cheeks and throat jet-black to dark grey. However, range in coloration of cheek continuous from white to black and taxonomic value of this character not firmly established (see Macaroni Penguin). Facial colour does not change with age after breeding age reached (Shaughnessy 1975). No other crested penguins have crests that meet on forehead. Only other penguin with white face is Chinstrap *Pygoscelis antarctica* which has slim black bill and no yellow on head.

Breed at Macquarie I. in huge colonies. Usually walk on land, but hop when hurried. Swim with head and part of back out of water; porpoise when swimming fast. Vagrants solitary or in small groups, often among other crested penguins.

HABITAT Marine, in subantarctic waters round breeding station; range at sea poorly known. In breeding season, main prey taken occurs in pelagic waters (Horne 1985); outside breeding season, birds assumed to be pelagic as absent from Macquarie I. and surrounding waters (Warham 1971b).

Colonies along shore, on scree slopes or among hills; up to 1.6 km inland and 150 m asl. Nest on open sandy, rocky or pebbly level ground, unvegetated; occasionally among talus of large rocks. Inland colonies may be linked to sea by creeks which are used as access routes from sea (Falla 1937; Warham 1971b).

DISTRIBUTION AND POPULATION Breed only at Macquarie I. and adjacent islets; occasional records Aust. and NZ. Precise wintering areas unknown but assumed to be in subantarctic waters near Macquarie I. (HASB). Identification of Royal and Macaroni Penguins difficult and status of white-faced birds at colonies other than on Macquarie I. not adequately determined.

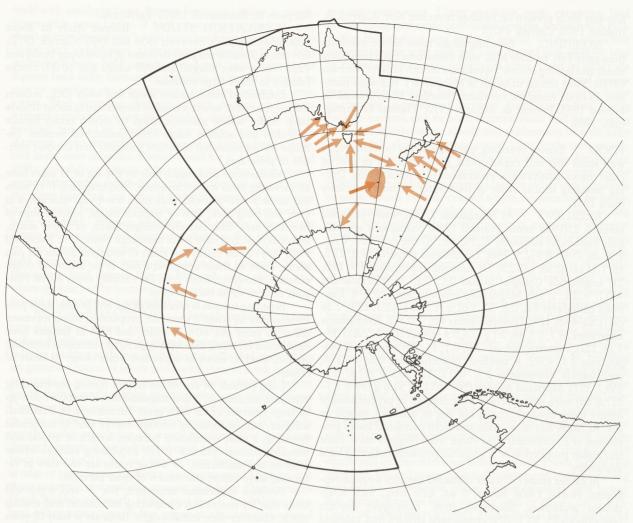
Occasional white-faced birds at Heard I. (probably Royals from Macquarie I.) and Iles Kerguelen. Small numbers of white-faced Royal/Macaroni Penguins have been found breeding in colonies of Macaroni Penguins at Marion I. (Voous 1963; van Zinderen Bakker 1971; Williams & Burger 1978; Berruti 1981) and most colonies on Ile aux Cochons and two localities on Ile de la Possession at Iles Crozet (Prévost 1970; Despin *et al.* 1972; Barré *et al.* 1976). Berruti (1981) cast doubts on some aspects of Voous's (1963) report at Marion I. and suggested that white-faced birds may be aberrant Macaroni Penguins rather than vagrant Royals.

Some black-faced birds that occasionally occur on NZ subantarctic islands probably Macaroni Penguins from Heard I. or Iles Kerguelen.

AUST. Vagrants to s. Aust., mostly Tas.

Vic.: W of Nelson Lagoon, June 1978–Mar. 1979 (Aust. Atlas); Apollo Bay, Feb. 1978 (Wheeler 1978; MV).

Tas. (from Tas. Bird Reps 1981, 1984–88 unless stated): Eaglehawk Neck, Feb. 1944 (Hindwood & Sharland 1944), Mar.-Apr. 1952 (Cashion 1953), Jan. 1981, 28 Feb. 1983, May



1984, 18 Feb. 1985; Coles Bay, Feb. 1945 (Sharland 1945); Adventure Bay, Mar. 1962 (TMAG); Falmouth, Mar. 1975, 1976 (Green 1977); Safety Cove, Mar. 1974 (Green 1977), Feb. 1977 (Aust. Atlas); Wilson Bight, Mar. 1976 (Aust. Atlas); Bicheno, 10 Feb.-8 Mar. 1981; Blackman Bay, 6 June 1981; Surveyors Cove, 28 Feb. 1983; C. Wickham, King I., Mar. 1984; Ketchem Bay, Feb. 1986; Risdon, Mar. 1987; Fortescue Bay, 19 Apr. 1987; King I., 23-26 Mar. 1988 (RAOU Newsl. 76).

SA: Encounter Bay, Feb. 1933 (B16739 SAM; Condon 1950).

NZ Stragglers claimed at Napier, Wellington, Waikouaiti, near Dunedin; one bird, Moeraki, 17-18 Mar. 1986 (CSN 34).

CAMPBELLI.: occasional visitor. Two, Jan. 1945; one, Mar. 1945; one, Jan. 1958 (Bailey & Sorensen 1962); four, 19 Jan. 1968 (Kinsky 1969).

SNARES I.: straggler, recorded on several occasions (Warham & Keeley 1969); one, 19-25 Feb. 1986 (CSN 34).

ANTARCTICA At least one record; two 'immature' intermediate phase came ashore to moult in Terre Adèlie, Feb. 1951; skin of one in Paris Museum (Jouanin & Prévost 1953).

BREEDING Generally considered restricted to

Macquarie I. but see discussion above of white-faced birds recorded elsewhere.

Macquarie I.: 1984–85, 848 719 \pm 10.5% pairs in 57 colonies (Copson & Rounsevell 1987).

Bishop and Clerk Islets: 1000+ birds in two colonies (Lugg et al. 1978).

On Macquarie I., colonies, reduced by past exploitation, appear to have recovered fully (Rounsevell & Brothers 1984).

MOVEMENTS Migratory or dispersive but movements away from Macquarie I. virtually unknown.

DEPARTURE Most adults leave after moulting early-mid Apr. (Carrick 1972), chicks having left first week Feb. (Warham 1971b), non-breeding immatures from third week Feb. onwards (Carrick & Ingham 1970; Carrick 1972).

NON-BREEDING Virtually nothing known of movements during non-breeding season but almost certainly absent from vicinity of Macquarie I. (Warham 1975).

RETURN Males arrive mid-Sept. (earliest 3 Sept.; Falla 1937; Warham 1971b), peaking late Sept.-early Oct. (Smith 1970; Carrick 1972). Females return about a week later. Younger birds return at increasingly later dates with last first-year birds present on beaches from late Nov. (Carrick & Ingham 1970; Carrick 1972).

Breeding adults leave before moulting BREEDING from early Feb. to early Mar. with immatures both beginning moult and leaving colony 3 weeks to a month earlier (Warham 1971b). Most return to moult at Macquarie I. but small numbers do so on Antarctic continent (Merilees 1970; Jouanin & Prévost 1953; Prévost & Mougin 1970; Thomas & Bretagnolle 1988).

During breeding, euphausiids fed to small chicks FOOD with small fish and cephalopods predominating in diet of older chicks. BEHAVIOUR. Food taken by pursuit-diving. During breeding season drink at freshwater streams in colony (Falla 1937).

At Macquarie I. (182 water-offloaded BREEDING samples; 210 955 items; Hindell 1988) crustaceans euphausiids Euphausia vallentini 32.1% wt., 57.8% no., 70% freq., 1.56 cm (0.47; 0.5-2.5; 746), Thysanoessa gregaria 10.3, 21.2, 18, 1.33 cm (0.38; 1.0-2.5; 33), unident. euphausiids 8.9, 18.8, 21, amphipods Cyllopus lucasii 0.1, 0.1, 16, Gammaridea <0.1, <0.1, 1; fish Magnesudis prionosa 3.6, <0.1, 4, Electrona carlesbergi 9.6, 0.8, 30, 1.62 g (1.7; 0.1-12.3; 129), 2.36 cm (1.62-4.48; 129), Gymnoscopelus 4.0, <0.1, 6, Krefftichthys anderssoni 23.7, 1.3, 48, 2.1 g (0.8; 0.4-4.4; 222), 2.51 cm (1.39-3.18; 222), Protomyctophum 3.8, 0.1, 14, Paranotothenia magellanica 0.1, <0.1, 4, unident. Nototheniidae 0.8, <0.1, 8; cephalopods Moroteuthis 2.1, <0.1, 11, 30.5 g (47.4; 0.1-259.7; 327), Martialia hyadesi 0.6, <0.1, 3, 51.6 g (54.3; 1.1-317.6: 65) were unimportant. Diet differed in proportions of dietary items between coasts but not in quantity, variety or size. At Bauer Bay on w. coast stomachs contained lower proportion of E. vallentini than those from Nuggets on e. coast and higher proportion of T. gregaria, probably reflecting local availability.

In earlier study (50 water offloaded samples without repetition; Horne 1985), fish 57% wt. 62% freq., incl. Krefftichthys anderssoni, Electrona, imm. Harpagifer bispinis; cephalopods 25, 30, 1-70 g; crustaceans 18% wt. incl. calanoid copepods, euphausiids 13% wt., 66% freq. (Euphausia similis 2% freq., E. vallentini 52, Thysanoessa gregaria 42), amphipods 5% wt., 66% freq. (Hyperia antarctica 2% freq., H. sp. 2, Themisto gaudichaudii 38, Primno macropa 50); arrow worms and seaweed. Samples from Bauer Bay, w. coast, contained fewer fish and euphausiids but more cephalopods and amphipods than those from Sandy Bay, e. coast. Data probably biased because stomachs flushed only once (Gales 1987) and no allowance made for different rates of digestion (Hindell 1988).

Mean weight adult stomach contents 249 g INTAKE (238; 211), 20–50 g being brought ashore before hatching and after moult but rising to peak of 668 g late Dec. (Hindell 1988).

SOCIAL ORGANIZATION At breeding sites in territorial pairs or solitary. No evidence of association with mates outside breeding period.

BONDS Monogamous; bonds long-lasting. No cooperative breeding.

BREEDING DISPERSION Colonial; size of colony ranges from 75-160 000 breeding pairs (Copson & Roun-Density at Lower Sandy Bay colony was 2.43 nests/m² wave flippers about. Attacked bird either retreats or defends

(Copson & Rounsevell 1987). Territorial.

POPULATION STUDY Intense study of about 2000 breeding pairs, between 1956 and 1970 (Carrick 1972); 884 adults (established pairs or mates of known-age birds) and 7223 chicks were marked and 990 adults and 10 000 chicks banded in three large colonies.

Established males return about first week Oct., reclaim former nest-sites, where joined by former mates about 10 days later. Males whose partners failed to return retain former nest-sites and acquire mates from unattached females. Females whose mates fail to return generally find another partner in same area.

Adolescence prolonged; only by the age of 11 years have all surviving birds started breeding. Non-breeders, 7-10 years old, some 5- to 6-year-old birds and a few 4-year-olds arrive in Oct. and hold sites, with or without mates, round fringe of breeding area. Successively younger birds, of lower status, arrive in Nov. and have fewer fixed sites. Some 1- to 3-year-old birds visit colony briefly but many of youngest do not get past shore; some in these age-groups may come ashore at other colonies. However, from then on virtually every Royal Penguin returns to its natal colony.

Breeding success is function of age and fitness; most precocious may lay when 5 years old; proportion laying increases till at 10 years old, 60% of males and 85% of females have established breeding sites with eggs. After successful breeding started, tend to move in successive years closer to heart of colony.

Long periods of starvation ashore during pre-breeding activities, incubation, guard-stage and moult involve build-up of large reserves of fat with great fluctuations of individual weights. Accumulation of enough energy vital to successful breeding; a clear correlation between weight at arrival and breeding success (Carrick 1972). Incubating females whose reserves are insufficient, or whose mates are too slow at returning leave before the return of their partners.

Previous experience important; few 5- and 6-year-old birds that lay succeed in completing incubation and rearing chick, whatever their initial weight. Birds are at least 10 years old before contributing regularly to annual production of fledged young, and even among established breeders only about 50% of pairs succeed in fledging their chick.

Survival of 4000 banded chicks at subsequent moults was at least 67, 43, 34 and 20% in first 4 years; in another colony, at 5, 6, 7 and 8 years of age, survival was 12, 10.4, 8.5 and 6.8%. Low productivity (one chick fledged for every four breeding adults over 10 years old) followed by survival of about 5% of these fledgelings to breeding age, indicated that best-established adults long-lived, with an even higher annual survival rate than 86% recorded. This suggested that success in intraspecific competition for a limited resource, probably food, is chief factor in population ecology of the species.

SOCIAL BEHAVIOUR Detailed studies by Warham (1971b) and Smith (1974). Displays very similar to those of Macaroni Penguins (Warham 1971b).

AGONISTIC BEHAVIOUR Usually at breeding grounds. Males more pugnacious. Close approach by individuals other than mate resisted. Intimidatory actions keep intruders out of pecking range: bird leans towards stranger by tilting head to one side and lowering hyoid, emitting staccato sevell 1987); however, small groups of breeding birds <250 m cry or hiss. May also bob head up and down and raise flippers from larger colony were included as part of larger colony. ready for use. If within range, may strike out with bill and

itself with similar actions. Sitting birds may strike at neighbours with open beaks. If beaks become interlocked, may develop into 'tug-of-war', with mate reaching over partner to bicker with neighbours. APPEASEMENT. Slender Walk: bird walks with body held upright, head and neck bowed, and flippers held stiffly forward and parallel. Adopted en route to nest or moulting site when moving between owners of territories. Bird hurrying through crowd dodges and pecks without retaliation; when surrounded, stretches neck above pecking range. On reaching clear space, performs Stare Around: stops abruptly, swings head up, raising beak a little, and looks over shoulder. Position held for c. 1 s before head stiffly jerked from side to side, with pause after each movement. Submissive Attitude. Incubating females do not retaliate when assaulted, but crouch with bill pressed to ground or tucked under body; maintain posture even as attacker pecks at nape and back. Flipper Flicking: bird rapidly flicks single flipper when undecided whether to fight or flee. Often used by non-breeders standing among established breeders or by bird away from nest when approached by intruder. Wing Shivering: bird shivers flippers through very narrow arcs when approached by human; usually does not flee; not known if used in response to natural threats.

SEXUAL BEHAVIOUR Sexual displays often contain element of threat; expression of sexual motivation may reduce likelihood of attack. Nest-formation: bird rotates on belly by pushing with feet, with flippers extended and resting on ground. Occurs at sandy and rocky sites; in sand, hollows are made in which birds incubate. Mostly observed before laying; infrequently during re-occupation and moult. Stone Carrying: birds carry stones and other objects such as bones to nest, often forming substantial accumulations. Generally only by males; most often on arrival at colonies but continues through breeding period and during moult. At sandy sites birds collect sand in bill and deposit round rims of nests. Birds at edge of colonies may collect tussock-grass and line nest, but these materials not available to most of colony. Quivering (= Head Wobble of Smith 1974): bird bends head down into nest, bill pointing towards feet, egg or chick; then shakes head rapidly through narrow arc while moving head and neck from one flank of body to other; chattering cries may be given throughout. Used by either sex; single birds or pairs; restricted to nest-site. Used by incubating females when mate adds stones to nest; by pairs standing on nest; by single birds returning to eggs or chicks after change-over. Often followed by Bowing and Head Swinging. Bowing: bird points head down into nest while uttering series of deep throbbing cries. Body shakes with each throb, flippers kept at sides. Pairs often reach over rim of nest with bills together. May follow Quivering and progress to Head Swinging. Used by lone birds or mated pairs; by both sexes throughout breeding season; restricted to nest-site. Shoulders-hunched Attitude: bird stands hunched over nest, flippers held stiffly forward, head bowed and bill open, shaking head vigorously and chattering (Voice). Mainly by males waiting for mates or when laying about to begin. Observed when bird returns to occupied or unoccupied nest after brief absence or before change-over with eggs or chicks. Also away from nest by pre-breeders starting temporary associations. Has sexual and submissive elements. Trumpeting: bird returning to nest after long absence changes gait from Slender Walk about 2 m from nest; hurries forward with neck and flippers outstretched, while braying loudly. Partner responds with similar cries, and reaches out from nest. Neighbours may copy, stretching out

towards newcomer. Upon reaching nest, returning bird pushes up against mate; both stand upright, throw heads back so that bills vertical, and trumpet loudly. Flippers raised and lowered in time with calls but head moved only slightly. May be repeated before nest-relief takes place. Used by either sex as mutual greeting and recognition ceremony. Head Swinging (= Flag Display of Smith 1974). Usually initiated by males to advertise ownership of territory. Head bowed then swung back to vertical, one or both flippers raised and head swung from side to side, either slowly and deliberately or with jerky actions; bill almost touches carpal joint with each stroke. Silent or accompanied by raucous pulsating cries. Sitting bird may respond with Head Swinging; females often respond by calling without Head Swinging. Used by either sex; lone birds or pairs; mainly by fully-crested adults, occasionally by immatures, yearlings; throughout breeding season and during moult. Not restricted to breeding colony; may occur wherever birds ashore. Follows arrival on territory; arrival of neighbour; female passing by; threats or displays of neighbouring birds; any disturbance. Frequency increases with density of colony. ALLOPREENING: mated pairs preen heads, necks and napes. turning heads to one side to reach each other simultaneously (Warham 1971b). Observed between members of opposite sex from 1-year-old onwards, between chicks in crèches, between members of temporary partnerships, indicating at least temporary acceptance, and between parents and feathering chicks. COPULATION. Mainly initiated by male by reaching towards mate's nape with bill and rapidly beating her on back with flippers; female subsides and allows him to mount. Male steps up and down on female, gripping with his feet and nibbling bill about mate's cheeks and neck, while continuing to pat her flanks with his flippers. Initially, tail swept from side to side but then depressed to make cloacal contact. Birds remain motionless during consummation; male then descends and stands still in Shoulders-hunched posture. Prone female also stays still. Mutual preening, head shaking and body stretching may follow. Copulation ceases among breeders after laying. but occurs between birds without eggs or chicks up to mid-Dec. UNCLASSIFIED POSTURES. Head Shake: bird shakes head quickly through about 60°; then makes swallowing movements; usually silent. Usually after period of excitement e.g. emergence from rough sea, fighting, display.

RELATIONS WITHIN FAMILY GROUP Similar to Macaroni Penguin (q.v.).

VOICE Not well known; descriptions in Warham (1971b) and reviews by Warham (1975) and Jouventin (1982) (including sonagrams of some calls). Like all crested penguins. noisy, demonstrative and aggressive at breeding colonies. Calls, mostly loud harsh braying or raucous cries given in various circumstances. Most calling at colonies during breeding season; increase in activity and noise with arrival of males and, later, females; colonies much quieter after laying, when males leave; brief barking Contact Call given through year, on land and at sea. Calls of all Eudyptes species similar; calls of Royal very similar to those of Macaroni Penguins (Jouventin 1982). Individual recognition. Jouventin (1982) showed that calls essential for individual recognition between mates and between adults and their chick. Sexual differences not clear; in field, many songs of males clearly distinguishable as being pitched lower than those of females but differences not evident from sonagrams of small sample (Jouventin 1982). Nonvocal sounds: loud slapping sounds made by flippers during agonistic clashes; male beats flippers rapidly against back and

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sides of female during copulation as in other Eudyptes.

ADULT No detailed analysis of calls associated with particular displays; Jouventin (1982) states that Ecstatic and Mutual Display Calls related and presumably similar but Warham (1971b) describes different calls for these displays. Ecstatic Call (Trumpeting). Loud sustained throbbing brays; infectious within colonies. Series of repeated phrases varying in length and consisting of brief pulsed notes. Usually begin with long, drawn-out, rapidly pulsed syllable; middle part of call, long series of short rapidly pulsed notes; call usually ends with long drawn-out rapidly pulsed syllable similar to first syllable (Jouventin 1982). Head Swinging Call. Series of raucous cries, similar to Trumpeting but sounding more pulsed. Bowing Call. Described as loud, deep throbbing cries. Quivering Call. Described as chattering cries. Squeal as given by Rockhopper not recorded (Warham 1975). Threat Call. Short burst of staccato cries; Jouventin (1982) shows two examples, each consisting of a long note followed by several brief pulsed notes; resemble abbreviated form of display calls. Contact Call. Short monosyllabic low pitched barking call; no sonagrams.

YOUNG Chicks beg with simple *cheep*; single note increasing then decreasing in pitch; duration *c*. 0.2–0.45 s. Calls begin to differ after chick leaves nest (Jouventin 1982).

BREEDING Well known. Major study by Warham (1971b). Information supplied by J.R. Starks. Breed in colonies of 10⁵ pairs round Macquarie I.

SEASON Birds return mid- to late Sept., males synchronized between 8–10 and 30 Oct. Hatching 21 Nov. to 10 Dec. Fledging, late Jan. to early Feb. Colonies deserted by mid-May (Warham 1971b; Watson 1975).

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SITE On open sandy, rocky or pebbly ground, flat or gently sloping without vegetation; from high-water mark to 150 m asl. Access to colonies along streams or up steep tussock-clad hillsides. Mean density of nests 2.43/m². Same site used year after year by same pair. Young birds tend to return to natal colony.

NEST, MATERIALS Shallow depression of stones or sand, sometimes lined with grass. Males start to collect pebbles soon after arrival; substantial accumulations may result. Nest formed by bird squatting on belly, pressing back with feet and rotating to form hollow; at sandy sites these may be quite deep and birds may incubate with sand banked round them. Stones and other material often added to by male during incubation or after change-over.

EGGS Spheroidal to elongate oval; rough textured, mat; chalky white. First egg (A) invariably smaller than second (B). Measurements and weights from Woehler (in press). MEASUREMENTS.

A-egg: 69.7 (3.04; 62.5-75.2; 31) x 50.8 (1.92; 47.5-56.2). B-egg: 80.7 (3.89; 72.0-88.0; 28) x 59.2 (2.11; 53.5-62.8). WEIGHTS: A-egg: 100.3 (10.54; 79.7-126.9; 31). B-egg: 159.3 (15.96; 125.6-181.0; 28). CLUTCH-SIZE Two.

LAYING Interval of 4-6 days between laying of A-

and B-eggs (Warham 1971b).

INCUBATION By both adults in alternate shifts; starts fully with B-egg; A-egg seldom incubated because birds fail to sit properly and often change over; usually destroyed or ejected before or soon after B-egg laid. Egg supported by feet and incubated in highly vascularized pouch-like brood-patch. Female takes first shift of 12–14 days; male, second also of 12– 14 days; female usually returns about a week before hatching and both birds present at hatching. If A-egg fertile, both eggs of clutch may hatch (Warham 1971b). INCUBATION PERIOD: 35 days (Gwynn 1953); 32–37 days (Watson 1975).

NESTLING Semi-altricial, nidicolous. Hatched in down. Brooded by male for 10–20 days, in brood-pouch; fed by female while male broods. Fed by incomplete regurgitation, with about two visits every 3 days. At about 3 weeks old, chicks become mobile and begin to form crèches; males then go to sea and both parents share feeding of chicks, which are fed only on nest; parents feed only their own chick. NESTLING PERIOD: about 65 days and crèches break up in latter part of Jan.; none seen after 25 Jan. (Warham 1971b).

FLEDGING TO MATURITY Growth rapid for first 3 weeks; down replaced with feathers about 5-6 weeks. Independent of parents after fledging. For development to maturity, survival of chicks and success rates, see Social Organization. Predation by skuas and Wekas Gallirallus australis. Southern Elephant Seals Mirounga leonina may invade colonies and destroy adults and young.

PLUMAGES

ADULT Definitive basic. Plumage generally assumed at third prebasic moult, but age of first breeding at least 5 years (Carrick & Ingham 1970). Polymorphic; females tend to be darker (see Geographical Variation). Tendency for birds to mate with others of similar facial colour which not related to age (Shaughnessy 1975).

Light morph. HEAD AND NECK. Crown, nape, hindneck. and sides of neck, blackish. Feathers have black (89) tips and rachis merging through concealed greyish brown (greyish 119B) to white bases. Forecrown, sides of mid-crown, and most of forehead, orange-yellow (18), heavily streaked black (89). Feathers, orange-yellow (18) with elongate narrow black (89) tips. Forecrown also has narrow plumes, 70-80 mm long, some running along line of supercilium, some drooping over face; these plumes orange-yellow (18) with fibrous texture formed by stiff rami running parallel to rachis. Patch on forecrown sometimes separated from bill by narrow strip of black (89) feathers. Feathers at base of bill below junction of culminicorn and latericorn, pale yellow (157). Chin, throat and facial area, white. Line separating dark crown from white face begins at junction of culminicorn and latericorn, and runs about an eye-width above eye. Demarcation of white face and blackish head unclear in birds in fresh plumage (Shaughnessy 1975). UPPERPARTS, mostly blackish. Feathers, blackish (82) merging through concealed greyish brown (greyish 119B) to white base. Rachis, black (89) at tip, white with blackishbrown central stripe at base. When fresh, feathers have small grey-blue (c88) tips. When worn, most birds develop white patch in central upper tail-coverts. Some central upper tailcoverts white, concealed by other feathers when plumage fresh. Dull 'bronzing' occurs just before moult (Warham 1971b). TAIL, blackish (82). UPPERFLIPPER, blackish (82) with narrow white trailing-edge from elbow to tip. Leading-edge, white. UNDERPARTS, white; separated from dark upperparts by straight line running below flippers. UNDERFLIPPER.

mostly white, with fine black streaking near trailing-edge caused by black (c89) shaft-streaks to some feathers. Large black (89) markings at tip and elbow. Black leading-edge of proximal underflipper runs for at least half length and often extends to tip.

Dark morph. Rather rare (see Geographical Variation) and probably indistinguishable from dark-faced Macaroni Penguin (e.g. Warham 1971a; Falla *et al.* 1981). HEAD AND NECK. Facial region and throat blackish (82) to black (89); black extends to centre but not sides of foreneck.

Intermediate morph. Continuous variation from light to dark morphs. Some birds as pale morph, but with pale brown-grey (greyish 119D) patches above eye, in interramal region or across lower throat. Darker birds usually lack lemon-yellow feathers at base of bill; dark patches larger, may cover all face and throat, and range from pale brown-grey (greyish 119D) to blackish (82). Generally area round and above eye is darkest.

DOWNY YOUNG Protoptile: smooth and rather sparse. Crown, forehead and lores, dark chocolate-brown (c119). Rest of head, and upperparts, medium brown (119A). Underparts, white, merging to pale grey-brown on upper throat. Upperflipper, pale grey-brown (119D) with white fringes. Underflipper, white with pale grey-brown (119D) leading-edge. Mesoptile: dense and woolly. Head, hindneck, upper throat and upperparts, dark greyish brown (greyish 121). Underparts and lower throat, white. White extends farther forward on sides than in centre of throat; sharp cut-off between white lower throat and dark-brown upper throat.

JUVENILE Feathers of forecrown and most of forehead yellow (157) with narrow black (89) tips. Patch on forecrown lacks elongate orange-yellow plumes of adult. Facial colour generally as intermediate adults; no records of wholly white-faced juveniles. Unknown if darkness of face as juvenile related to darkness of face as adult.

IMMATURE Similar to intermediate adult, but yellow plumes of crest may be noticeably shorter (Warham 1963, 1971b). Usually lack white spot on upper tail-coverts (needs confirmation).

ABERRANT PLUMAGES Melanism and albinism recorded (Falla 1937).

BARE PARTS Based on label data (NMNZ), Warham (1971b) and photos (Lindsey 1986; Peterson 1979; Harrison 1987; P.J. Moors).

ADULT, IMMATURE Iris, crimson (110) merging to brick-red (132A) outer ring. Base of bill has margin of fleshy skin below junction of culminicorn and latericorn; in some individuals, this strip narrow and inconspicuous in narial groove. This strip, and rictus, usually pink (7) ranging from dull pink (5) through peach-red (94) to pinkish red (108B). All plates of bill have narrow margin to base, broadest on culminicorn; pale grey (86) to dark grey (83). Tip of upper mandible has small pale orange-buff tip. Colour of rest of bill varies, tending to be darker in dark-faced birds; from light orange-rufous (orange 119D) through peach-red (94) and rufous (41) to mahogany-red (132B to rufous 4). Culminicorn usually slightly paler than other plates. Tarsus and upper side of feet, flesh (5) to pink (7). Soles, black. Claws, dark grey (83) to dark grey-brown (22), often with pink (7) patch on centre and base; sometimes claws entirely pink (7). Many birds have some dark-grey and some pink claws.

DOWNY YOUNG No information on protoptile, but probably similar to Macaroni Penguin (*q.v.*). In mesoptile, iris, blackish brown (c20). Bill, blackish (82).

JUVENILE Iris usually brown (22) to dark brownish-olive (129), but can be almost as red as adult (Warham 1971b). Rictus and fleshy skin at base of bill coloured as adult; often strip of fleshy skin too narrow to be seen easily. Bill varies; usually as adult but can be pink-brown (221D). Dull brown also reported (Warham 1971b).

MOULTS Based on Warham (1971).

ADULT POST-BREEDING Definitive pre-basic. Complete, at nest-site, after almost 5 weeks at sea. Duration ashore 24–29 days; first feathers lost 4–6 days after returning to nest, and last old feathers lost 15–19 days after first. Rectrices still growing at this stage. Successful breeders first return to moult in first week Mar.; numbers peak in second week Mar. Colonies half empty by mid-Apr.; last moulters leave by May.

POST-JUVENILE By last week Jan. many birds have started to shed feathers and some have moulted. Most have moulted and left by last week of Feb.

PRE-BASIC OF NON-BREEDERS AND UNSUC-CESSFUL BREEDERS Presumably moult between breeders and juveniles, because breeders last birds to moult, and older immatures outnumber juveniles in third week of Feb.

MEASUREMENTS (1) Macquarie I., adults, breeding status unknown, skins; FLIPPER from posterior side of axilla to tip; bill measurements as recommended and illustrated by Warham (1972, 1975); BILL = culmen length from tip to junction of culminicorn and skin at base; BILL W taken at widest point of culminicorn and skin at base; BILL D at junction of gonys and interramal region (MV). (2) Macquarie I., adults (face colour unknown), live; methods unknown (A. Gourin in Warham 1971b). (3) Macquarie I., adults, including darkphase birds, skins; flipper method unknown, TARSUS = maximum length from front (Falla 1937). These measurements inconsistent with observations that males always largest bird of pair (Warham 1971b; Shaughnessy 1975), which strongly suggests that some of Falla's birds incorrectly sexed.

		MALES	FEMALES	
FLIPPER	(1)	189.6 (4.45; 183-195; 5)	185.1 (8.79; 176-203; 7)	1
	(3)	217.5 (5.98; 205-225; 8)	215.7 (8.08; 200-223; 7)	
TAIL	(3)	97.9 (9.49; 80-107; 8)	87.8 (21.0; 55-108; 5)	
BILL	(1)	65.6 (1.62; 64.2-68.6; 5)	60.7 (2.01; 58-65.5; 9)	**
	(2)	66.4 (65-70; 10)	57.8 (55-64; 10)	
	(3)	65.8 (4.53; 60-73; 8)	65.8 (6.43; 57-74.5; 7)	
BILL D	(1)	28.0 (1.19; 26.2-29.9; 6)	25.9 (1.44; 24.1-29.1; 9)	**
	(2)	32.8 (31-34; 10)	29.4 (28-32; 10)	
BILL W	(1)	12.2 (0.41; 11.7-12.8; 6)	11.2 (0.90; 10.1-13.5; 10)	*
TARSUS	(3)	31.9 (2.17; 30-35; 8)	33.7 (2.50; 30-38; 7)	
TOE	(1)	79.7 (1.09; 78.8-81.5; 4)	76.0 (1.74; 73.0-79.2; 7)	**
	(3)	75.4 (4.24; 68-80; 8)	77.6 (5.38; 71-80; 7)	

WEIGHTS Adults, when feeding chicks: males c. 4.5 kg; females c. 4.0 kg (Warham 1971b).

STRUCTURE No occipital crest. Bill, long and heavy; upper mandible has hook at tip fitting into recess in lower mandible. Groove between latericorn and culminicorn deep, feathered at base. Tail short, 14 feathers. Middle toe longest,

outer *c*. 90%, inner *c*. 65%. Hind toe dangles on inner side of foot.

GEOGRAPHICAL VARIATION Often considered to be subspecies of Macaroni Penguin (q.v.). On Macquarie I., higher proportion of dark-faced birds on w. coast than on e. coast; situation intermediate on s. coast. In 498 pairs on e. coast (Sandy Bay, Red R., Green Gorge) 8% of females and 0% males had dark faces (eye and throat uniformly grey to black); 40% of females and 16% of males had intermediate faces; 52% of females and 84% of males had white faces. Of 450 females and 483 males in colonies on w. coast (Aurora Pt, Flat Creek, Bauer Bay), 56% of females and 11% of males had dark faces; 43% of females and 74% of males had intermediate faces; 2% females and 15% males had white faces (Shaughnessy 1975).

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Volume 1 (Part A), Plate 11 [caption errors corrected from original]

Royal Penguin *Eudyptes schlegeli* 1. Adult, light-faced morph 2. Juvenile 3. Downy young

Macaroni Penguin *Eudyptes chrysolophus* 4. Adult

- Rockhopper Penguin *Eudyptes chrysocome*5. Adult, subspecies *filholi*6. Adult, subspecies *moseleyi*7. Juvenile, subspecies *filholi*8. Downy young, subspecies *filholi*

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