

Order SPHENISCIFORMES

Family SPHENISCIDAE penguins

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

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

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

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

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

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

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

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

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

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

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

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

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

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Megadyptes antipodes Yellow-eyed Penguin

COLOUR PLATE FACING PAGE 208

Catarrhactes antipodes Hombron and Jacquinot, 1841, *Annls. Sci. nat., Zool., Paris, ser. 2*, 16: 320 —
Auckland Islands.

MONOTYPIC

FIELD IDENTIFICATION Length 56–78 cm; flipper 20–22 cm. Tall, distinctive penguin of s. NZ. Head, pale yellow, each feather with central black streak, and band of clear yellow passes across nape from eye to eye. No crest. Secretive, nesting solitarily under coastal vegetation. Sexes similar. No seasonal changes. Juveniles separable.

DESCRIPTION ADULT. Feathers of crown, sides of

face and chin, pale yellow, each with central streak of black; black predominates on crown, but can vary. Band of yellow feathers extends from gape, passing round eyes and encircling hindcrown. Sides of head and foreneck, light fawn-brown with darker edge below eye. Back and tail, uniform slate-blue, lighter than flippers. Chest and undersides, white, sharply separated from yellowish throat. Upper surface of flippers,

slaty blue-black with thin (2–3 mm) white leading-edge extending from axilla for about two-thirds of length of flippers; trailing-edge has broader band of white (4–6 mm) from carpal to tip; undersides, completely white. Bill, long and slender; upper mandible, red-brown; lower mandible, pale cream basally, toning to red-brown of upper bill. Eyes, yellow. Feet, pale pink but become brilliant magenta after strenuous exercise; undersides of feet, black; claws and edges of web, black-brown. Plumage duller just before moult (Feb.–Mar.). **IMMATURE.** Similar to adult but without yellow band of feathers round hindcrown; eyes, pale grey-yellow; chin, white.

SIMILAR SPECIES Distinctive yellowish head, yellow eye, and clear yellow nape separate adults from all other penguins. Juveniles less distinctive; pale eye and pale nondescript head markings distinguish them from other similarly sized penguins. Larger than sympatric Fiordland *Eudyptes pachyrhynchus* and Little *Eudyptula minor* Penguins. **At sea,** look for yellow band passing from bill through eyes and round nape, also large size, slender pinkish bill and slender neck.

Mostly sedentary. Gregarious in winter, many (50–100) congregating on upper beaches of major breeding areas before departure for, and after return from, daily foraging. Less gregarious during breeding season: nest solitarily but non-breeding adults and juveniles congregate in small groups on beaches or at loafing sites. Virtually no information on behaviour at sea; nearly all sightings of solitary birds. Most birds return to landing sites in ones or twos and probably forage alone. Sensitive to disturbance on and near shore when coming to land. On mainland, where people are about on beach, birds will congregate 200–300 m offshore, until beach clear. At subantarctic islands, when Hooker's Sealions *Phocarctos hookeri* present, form similar groups (10–20) and then make dash for beach when opportunity offers; and occasionally feed as group (P.J. Moore). Throughout year, found near scrubby and forested slopes where they breed; usually at nightfall come ashore onto rocky and sandy beaches and may climb over difficult ground to top of cliffs and breeding areas beyond. Timid and secretive nester, usually in dense vegetation. Walk with typical upright waddling gait of penguins. Rapid swimmer; porpoise often when near shore. Calls semi-musical, unlike harsh calls of most other penguins.

HABITAT Seas round s. SI, NZ, and neighbouring cool temperate subantarctic islands, from 43–52°S. Resident, remaining near breeding sites throughout year. Foraging range probably small because birds return to shore each night (Richdale 1941); on Campbell I. observed fishing close inshore (Westerskov 1960); may site colonies where continental shelf widest and most productive (J.T. Darby). Remain on land in day during rough weather (Richdale 1941).

Breed coastal s. NZ and islands; prefer small bays and headlands of large bays, nesting on shores, sea-facing slopes, hills, gullies and cliff tops (Guthrie-Smith 1914; Richdale 1941; Bailey 1955; Westerskov 1960); from near sea-level to 250 m asl. Usually within dense vegetation.

May prefer to land where immediate access to forest; so stretches of soft sand and shingle avoided (Guthrie-Smith 1914), but birds observed crossing 120 m of steep soft sand to edge of forest and appear to be good travellers on land (Richdale 1941). Of 42 landing sites on mainland, 55% on rocky shores and platforms, 45% on sandy beaches; of 172 on Campbell I., 39% on rocky shores, 61% on shingle or those with

small boulders (P.J. Moore). Access to nesting area may be steep; climb cliffs up to 90 m high (Bailey 1955; Richdale 1941). Can dive to at least 100 m (6 birds trapped in fishing net at this depth); mean max. diving depth 34 m (8; 19–56; 43) for 24 birds during incubation when feeding on bottom-dwelling fish (Seddon & van Heezik 1990).

Endangered on mainland. Almost all forest on se. coast SI cleared for agriculture. Formerly confined to podocarp-hardwood forest, but has spread into previously unoccupied habitats (scrubland, open woodland, pasture) since clearing of forest. In farmland, cattle trample nests, and nesting birds, particularly chicks, vulnerable to introduced predators.

DISTRIBUTION AND POPULATION Endemic to NZ; coasts of Otago and Southland, and on Auckland, Stewart and Campbell Is. Reach Cook Str. (NZCL) and, occasionally, NI.

Normally e. and se. coasts of SI, more commonly from Bluff to N of Oamaru, also Banks Pen., Stewart and Codfish Is. SI bird recorded Riversdale Beach, NI (Richdale 1957). Unverified reports from Chatham Is (Gray 1862; Ogilvie-Grant 1898; Sharpe 1899), Iles Kerguelen (Filhol 1885), Snares Is (Sutherland 1920) and Macquarie I. (Sutherland 1920).

BREEDING, POPULATION Disjunct breeding distribution; on mainland: SI, including Banks Pen. and se. coast from Oamaru to Slope Point; Stewart I., Codfish I., Auckland I. and Campbell I. Northernmost breeding records at C. Campbell (S of Blenheim), but only one breeding record in period 1969–79, Mar. 1971. (NZ Atlas). Probably solitary breeders (J.T. Darby *cf.* Richdale 1951, 1957) but breed in specific areas and use communal landing areas.

SI Known breeding sites and estimated numbers of breeding pairs, at Mar. 1990:

Canterbury:

Banks Pen.: 5 pairs.

Otago North: Oamaru S to Dunedin: 38

Bushy Beach: 6

Moeraki Pen.: 12

Katiki Beach: 6

Shag Point: 3

Bobbies Head: 6

Hayward Beach: 5

Otago: Dunedin and Otago Pen.: 198. As result of a number of unexplained deaths (120–140) of adult birds in Jan. 1990, perhaps total ought to be reduced by 60–70 pairs.

Penguin Beach: 26

Reids Beach: 6

Pipikaretu Beach: 17

Ryans Beach: 16

Victory Beach: 6

Dicks Beach: 3

Papanui Beach: 22

Alfred and Cecily Beach: 6

Sandymount Reserve: 3

Sandfly Bay: 12

Waterfall Bay: 1

Double Bay: 26

Boulder Beach: 28

Highcliffs: 12

Green Island: 14

Otago South: Owaka and Catlins: 79

Nugget Point Reserve: 18

Sandy Bay: 5
 Heywards Point: 7
 N. Jacks Bay: 2
 Tunnel Rocks: 5
 Penguin Bay: 5
 Hinahina Cove: 5
 Long Point: 11
 Falls Creek: 18
 Slope Point: 3

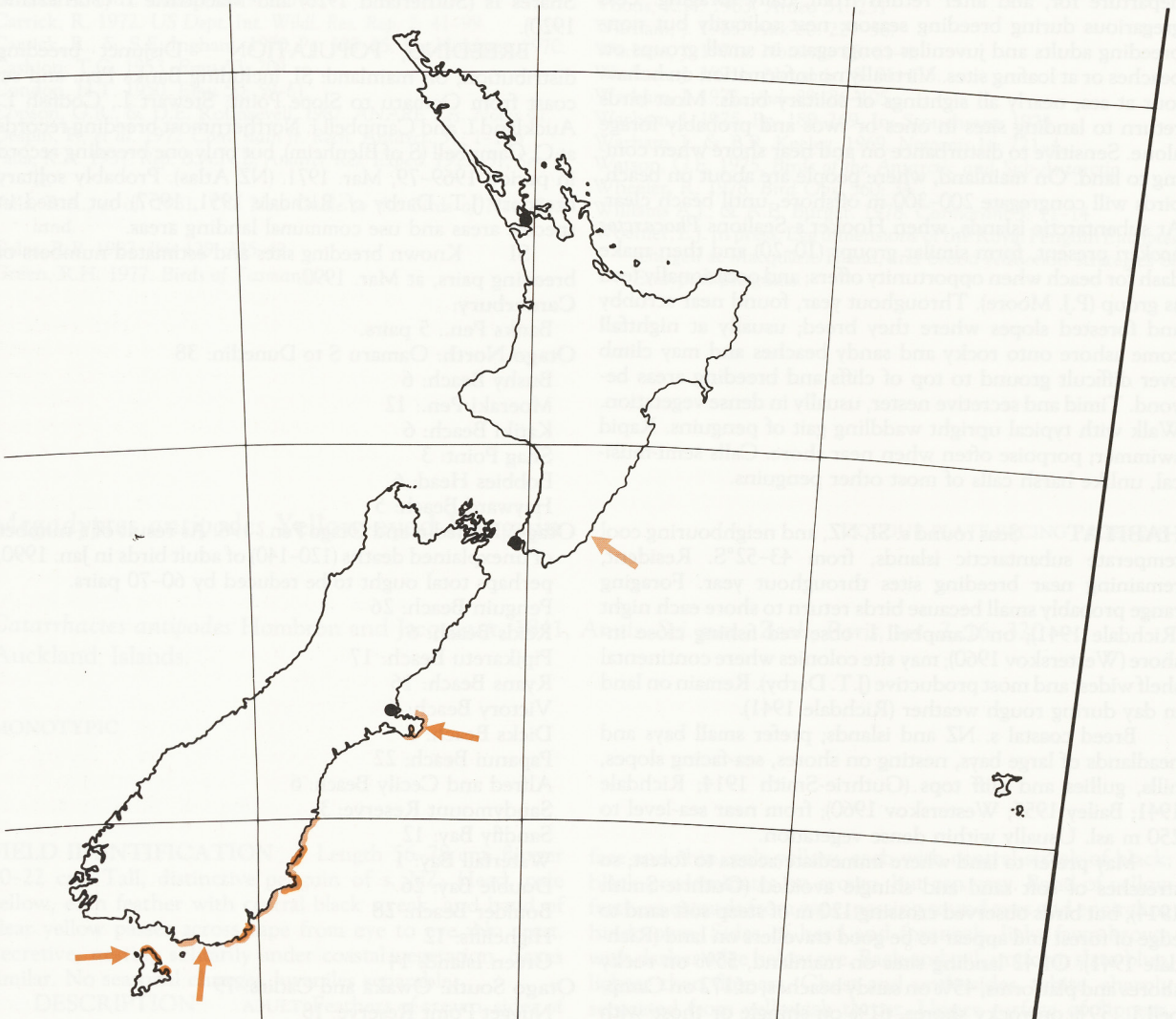
Total pairs: mainland, 300-320; Stewart I., 300-400; Auckland I., 250-350 (J.T. Darby); Campbell I., 560-700 (P.J. Moore). Total breeding pairs, 1410-1770.

Non-breeding birds, 1208-1517 (considered as 3% of total population [J.T. Darby; P.J. Moore]). Total population, 4028-5057.

Historically populations have fluctuated but these fluctuations poorly documented and not well understood. With time, breeding numbers appear to have been fairly stable. Between 1986 and 1987, breeding pairs on SI declined by 65%, probably with similar decline on Stewart and Codfish Is. Possibly due to shortage of food during summers of 1986 and 1987 (J.T. Darby).

Status, endangered on mainland, rare throughout rest of range and possibly threatened; Campbell I. holds about 34% total population (P.J. Moore). Totally protected. Breeding populations on e. coast and Southland threatened by almost total clearing of breeding habitat. Cattle trample nests; on Otago Pen. in 1985, 29 of 41 nests destroyed by cattle (J.T. Darby). Sheep cause less damage but modify habitat to suit lagomorphs, which in turn attract predators of chicks. Introduced predators at all main breeding areas; on Stewart and Campbell I., cats and rats; on Auckland I., cats, goats and pigs; little knowledge of levels of predation on chicks in these areas; apparently very low levels of predation on Campbell I. (P.J. Moore). Predation of chicks on farmed areas is high, exceeding 90% in some areas and years; feral cats and ferrets are considered responsible (J.T. Darby). Frequently captured in near-shore fishing nets; of 102 recoveries, 25% taken from set nets; autopsies of 112 birds showed 35% had drowned, of which 27% came from set nets (J.T. Darby).

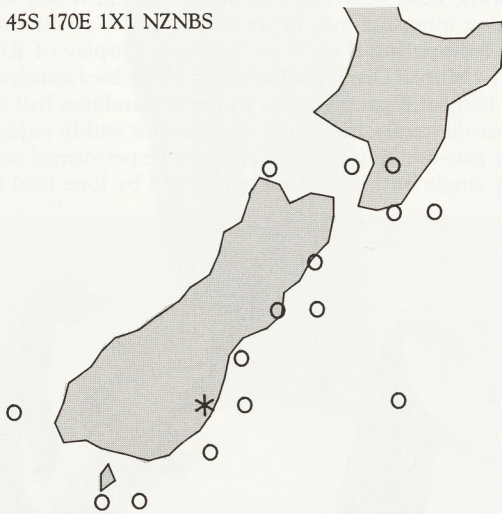
MOVEMENTS Sedentary, most adults wintering on or near breeding grounds. Juveniles fledge 10 Feb.-25 Apr. (Richdale 1957; J.T. Darby) and disperse N of natal area as do a



few adults, at least as far as Wellington, 600 km N, and through Cook Str. From degree of plumage wear, most of time thought to be spent at sea (J.T. Darby) though some stop for brief periods ashore (Richdale 1957). Surviving juveniles return to SI, 90% to within 10 km of natal area (J.T. Darby), from July onwards with small proportion spending summer in n. waters. Similarly, fewer juveniles seen Campbell I. in winter than in summer (P.J. Moore). Adult movements during non-breeding season thought to be limited to foraging trips of 1-3 days. Bird released 87 km from breeding site returned in 48 h, and when again released 350 km away returned in 17 days (Tunnickliffe 1979).

BANDING Returns from s. SI (NZNBS) summarized Fig. 1. Most live and dead recoveries of juveniles banded SI, from Banks Pen. (270 km N) and Kaikoura Pen. (439 km N).

Fig. 1. 45S 170E 1X1 NZNBS



FOOD Mostly fish with some cephalopods and very few crustaceans. **BEHAVIOUR.** Food obtained by pursuit-diving from surface using flippers, with all observations being of birds feeding alone. Most adults feed during day: when breeding, may return any time of day but usually after 12:00. During guard-stage, relieved bird leaves to forage in afternoon, returning at dusk; during non-breeding season, most leave at dawn, return 1-2 h before dark on SI (J.T. Darby). Some adults and juveniles at sea overnight but not known whether they feed then (J.T. Darby).

ADULT Samples from all major breeding sites (281 stomachs; Y. van Heezik) fish 87% wt, 91% no., cephalopods 13, 9. Fish were *Sprattus antipodum* 11% wt., 17% no., 70% freq., <2.0-16.0 cm, *Argentina australiae* 5, 5, 15, 0.3-2.1 cm, *Auchenocerus punctatus* 7, 10, 17, 2.0-18.0 cm, *Pseudophycis bachus* 32, 40, 49, <2.0-22.0 cm, *Parapercis colias* 7, 1, 7, *Hemerocoetes monoptygius* 21, 11, 42, <2.0-32.0 cm; cephalopods: *Nototodarus sloanii* 12, 8, 46, <1.0-18.0 cm. Diet varied both with season and locality. *Auchenocerus punctatus* occurred in diet only June and July. In n. breeding localities, *A. australiae*, *P. bachus* and *H. monoptygius* considered important for breeding; at s. sites, *S. antipodum* and *P. bachus*.

CHICK Diet resembles that of adults. Immatures (59 stomachs; Y. van Heezik) take more cephalopods *N. sloanii* (49% wt., 44% freq.) and fewer fish (*S. antipodum* 3, 59, *A.*

australiae 3, 7, *A. punctatus* 3, 27, *P. bachus* 29, 58, *P. colias* 7, 5, *H. monoptygius* 2, 39).

INTAKE Meal size: adults 340 g (390; 0-3319; 281), juveniles 366 g (648; 0-3954; 648) with 5% of all meal weights >10% body weight. Though no variation in weight of meals throughout year, trend for larger meals during moult, incubation and early guard-stage of chick (Y. van Heezik). Mean daily weight gain, 67 g (Richdale 1957). All hard parts of fish in diet digested within 24 h of ingestion (van Heezik 1988).

SOCIAL ORGANIZATION Solitary breeder. Gregarious in winter, which appears to be time of greatest social interaction between individuals at breeding sites. May congregate on upper beaches of major breeding areas before departure for, and after return from, daily foraging. Less gregarious during breeding season. Scattered, well hidden and small defended nesting territories mean that interactions between neighbouring pairs rare. Non-breeding adults and juveniles congregate in small groups on beaches or at loafing sites during breeding season. Virtually no information on behaviour at sea; nearly all sightings of solitary birds. Most birds return to landing sites in ones or twos and probably forage alone; for grouping offshore, see Field Identification.

BONDS Monogamous. Pair-bonds usually long-lasting; 27% of pair-bonds last for single season, 61% for 2-6 seasons, 12% for 7-13 seasons (Richdale 1957). Breakdown of bonds may be due to disappearance of mate or to new pairing. Known divorce accounts for c. 13% of pair-bond changes. Divorce rates increase at high nesting densities. About 62% population composed of breeding birds, 26% non-breeding adults and 12% juveniles (Richdale 1957). Sex ratio assumed to be 1:1 at hatching, but greater longevity and lower mortality in males creates imbalance with age. Male:female ratio 1.00:1.04, at 2 years of age, 1.00:0.89 at 6 years, 1.00:0.50 at 10-12 years. At 2 years old, 8% of males and 48% of females start breeding. Skewed sex ratio means that, though females tend to breed every season, males do not. Precise time of pair-formation not known, but first nest construction seen in June-July and most pairs for a season thought to have formed by pre-egg stage or shortly afterwards. Both parents incubate and tend young until fledging.

BREEDING DISPERSION Solitary. Distances between nests vary with density of vegetation; 20-100 m in open areas with high canopy, less than 20 m in dense low scrub; about 22 m in scrub at Campbell I. Spacing appears to reflect selection of sites with dense vertical cover and high degree of lateral concealment. Densities of nests recorded: 1 pair/ha in native podocarp-hardwood forest; 2-2.5 pairs/ha in modified forest-scrubland; 3-4 pairs/ha in Flax *Phormium tenax* pasture-tussock. In pre-egg stage, up to 20 m round nest site may be defended by pairs; during incubation and guard-stage, only immediate area round nest defended. Territories break down at end of guard-stage because chicks start to move about. Many territories may be defended throughout year (J.T. Darby). Loafing sites used throughout year, but appear to be areas of general use in which territorial defence does not occur. Some pairs may defend two nest-sites during pre-egg stage. Such sites usually close together, and may be used in alternate years, or one site used for incubation and other used in latter part of guard-stage.

ROOSTING Communal roosts on flat open ground in non-breeding period and for non-breeding birds in

breeding season. Paired birds roost at nest-site. Breeders return to nest at night and depart at dawn.

SOCIAL BEHAVIOUR Based mainly on Richdale (1951), Jouventin (1982) and study by P. Seddon. Information supplied by P. Seddon. Extremely wary of human presence; will not land on beach if humans in sight, and birds can only be easily approached at nest during incubation and early guard-stage. Hides essential for observations of displays. Seldom can more than two nests be seen from single vantage point because nests are so far apart and in dense cover. Movement of chicks through dense vegetation in post-guard stage hampers long-term observations. No information on flock behaviour; in groups that are preening, individuals sometimes allopreen; often depart for sea *en masse*, possibly because sealions are present (P.J. Moore). During preening at landing or loaf sites, individual distances c. 0.5 m, but may be reduced or temporarily ignored when moving along narrow access paths. Individual distances extended to c. 2 m round nest during breeding season.

AGONISTIC BEHAVIOUR **THREAT DISPLAYS** in increasing order of aggressiveness: Shoulder-hunching, Alternate-staring, Glaring, Gaping and Open-yell, which leads to combat. **Shoulder-hunching**: neck lowered, head and bill directed forward, shoulders raised, body leaning forward and flippers held forward; usually a static posture when used as threat display; usually a low-intensity display, possibly reflecting indecision (conflict) because may occur in submissive and sexual circumstances often accompanied by Throbbing call (see Voice). **Alternate-staring**: head moved slowly from side to side; each eye alternately presented to opponent; crown feathers may be erect and eyes widened; response to close persistent intrusion. **Glaring**: closed bill pointed directly at opponent; leans body forward, neck extended, crown erected and eyes open wide. **Gaping and Open-yell** (Fig. 2). As for Glaring, but with open bill; may be accompanied by loud harsh single-note call. If neither bird retreats, **PHYSICAL COMBAT** ensues: Charging, Tête-à-tête, Pecking and Grabbing, and Flipper-striking. **Charging**: defending birds moves towards opponent with steps or short run, body upright, head forward, crown erect, eyes wide; bill may be open or closed. **Tête-à-tête**: pecking at head of opponent, usually falling well short; opponent usually returns action and birds stand facing each other, bills almost touching; possibly an extension of Gaping. **Pecking and Grabbing**: bill strikes or nips feathers and skin of opponent's head and neck. **Flipper-striking**: rapid, hard blows with leading-edge of either flipper to anywhere on opponent's body. **APPEASEMENT**: Slender-walking, Hunched-walking, and Salute, Sheepish-look and Gawky Attitude Displays. **Slender-walking**: bird walks with body upright, flippers held forward, neck extended vertically, and bill held forward and parallel to ground; used when approaching conspecific, including mate; sometimes precedes Salute. **Hunched-walking**: posture as for Shoulder-hunching, but with bill pointing downwards and sometimes held near ground; also used while taking short steps towards conspecific and often precedes Saluting; possibly a more intense form of Slender-walking. **Salute** (Fig. 3) (Bowling of Jouventin 1982): bill held vertically with neck fully extended and flippers forward; bird, usually male, walks rapidly c. 1 m past conspecific, usually by Hunched-walking, then Salute for c. 5 s, after which neck and bill lowered, usually by Hunched-walking, then Salute for c. 5 s, after which neck and bill lowered, and head turned over shoulder to look at recipi-

ent of display. **Sheepish-look**: body and neck held upright, flippers forward and bill hung down parallel to neck; head may be turned to one side; also associated with nest-relief. **Gawky Attitude** (Fig. 3) (Bowling of Jouventin 1982): similar to Slender-walk, but given in response to Saluting. Juveniles appear to be subordinate to all adults. No information on other hierarchies.

SEXUAL BEHAVIOUR Pair-formation and maintenance of pair-bond achieved through nest-relief ceremonies: Throbbing, Shaking, Half-trumpeting and Ecstatic Display, and Mutual Preening and Mutual Nest-building. **Throbbing**: rapid pulsation of skin and feathers at base of neck; bill raised c. 45°, opened slightly, crown held erect; associated with grunt-chuckles. **Shaking**: head turned down to one side with partly opened bill held parallel to ground; crown erect, eyes open wide, flippers raised forwards and sideways; head movement caused by bill-quivering with increasing intensity; may be accompanied by a vibrating call. **Half-trumpeting** (Fig. 4) (= Welcome Display of Richdale 1951; = Mutual Display of Jouventin 1982): bird stands on toes with body or flippers slightly forward; mandibles half or fully open; calls loudly; may occur separately or within sequence of other pair-bonding displays, and may be performed mutually or by single bird; not often performed by lone bird at nest

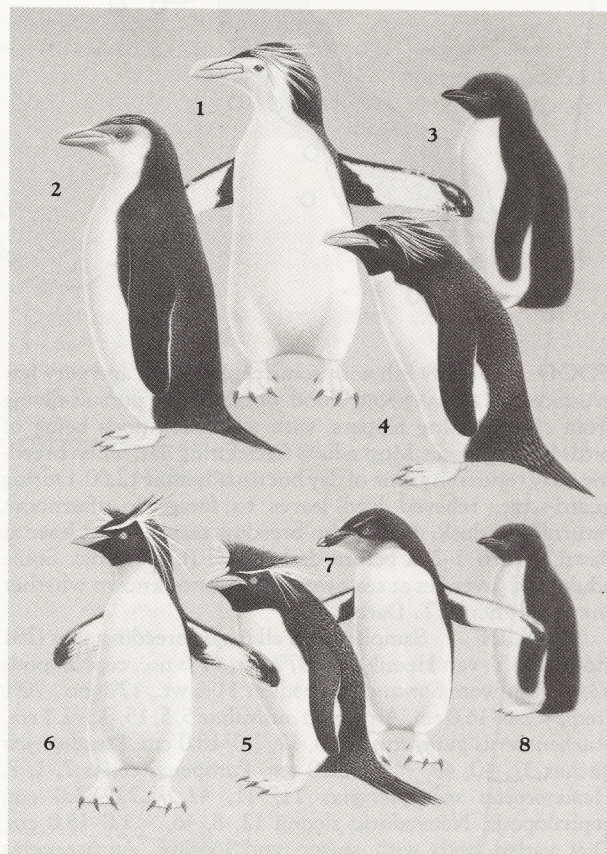


Plate 11

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

4. Adult
Rockhopper Penguin *Eudyptes chrysocome*
5. Adult, subspecies *filholli*
6. Adult, subspecies *moseleyii*
7. Juvenile, subspecies *filholli*
8. Downy young, subspecies *filholli*

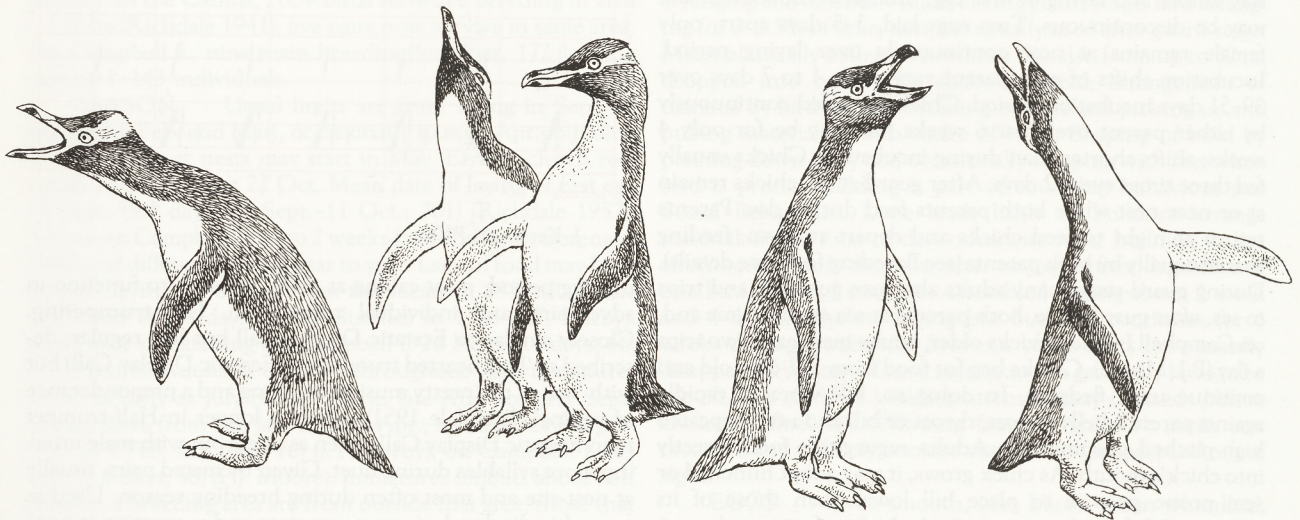


Fig. 2 Gaping and Open-yell

Fig. 3 Salute (left) and Gawky Attitude (right)

Fig. 4 Half-trumpeting

Fig. 5 Ecstatic Display

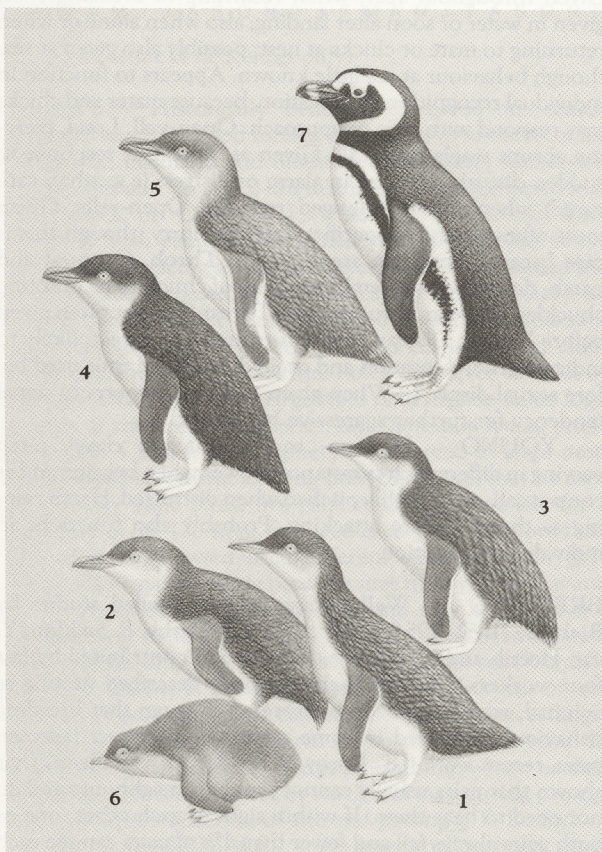


Plate 12

Little Penguin *Eudyptula minor*

1. Adult, subspecies *novaehollandiae*, fresh
2. Adult, subspecies *novaehollandiae*, worn
3. Juvenile, subspecies *novaehollandiae*

4. Adult, subspecies *minor*, fresh
5. Adult, subspecies *albosignata*, fresh
6. Downy young, subspecies *novaehollandiae*

- Magellanic Penguin *Spheniscus magellanicus*
7. Adult male

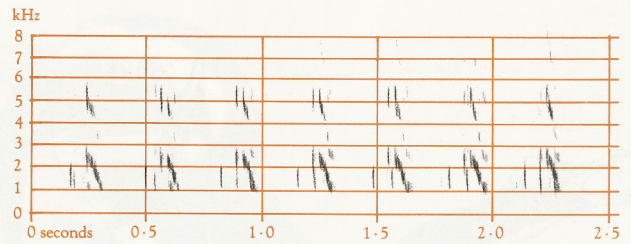
during breeding; may be very common when pair together; used as GREETING at nest; birds often approach nest by Hunched-walking before Half-trumpeting, and may end with Sheepish-look. **Ecstatic Display** (Fig. 5) (= Full Trumpet of Richdale): bird stands on toes with tarsi and tibiae erect, flippers held stiffly forward, head and open bill vertical, while emitting loud trilling call; bill vibrated and feathers and skin at base of throat and upper breast pulsed in and out; often culmination of other displays; usually given by lone bird on nest, especially males during pre-egg stage; may be spontaneous or in response to calls of, or intrusion by, neighbouring birds. **MUTUAL PREENING**: neck and head of mate or chick preened; includes preening of throat (kiss-preening). **Mutual Nest-building**: ritualized behaviour where one bird, usually male, collects and delivers small amounts of material to nest-bowl and then distributes material round nest; may be accompanied by displays of nest-relief ceremony; most common in pre-egg and early incubation stages. **COPULATION**. Only one complete sequence recorded (Seddon 1989). Male began behaviour by approaching female in Shoulders-hunched posture. Female moved away and adopted same posture. Male then followed and both birds circled nest several times before female stopped upright in nest-bowl, with back to male. Male then vibrated flippers lightly and rapidly against female's sides (arms act of Richdale 1951) once he had approached her from behind. Male then leaned forward against female and began to preen her neck. In response, female lay prone, braced feet backwards, extended flippers to sides, held tail vertically, everted cloaca and held neck upright with head and bill horizontal. Beating of flippers and preening continued as male climbed on female's back. Female maintained posture as male trod backwards, bowing his body and lowering his tail until cloacae were held briefly together. Immediately afterwards, male dismounted and began to preen; female remained prone for another minute before standing and preening also. Time from male's approach to dismount 110 s. Frequency of copulation unknown, but observed 12 days before first egg laid.

RELATIONS WITHIN FAMILY GROUP Both sexes take part in nest-building. Up to 21 days between first

stay ashore and laying of first egg, though occupation of site may be discontinuous. Two eggs laid, 3–5 days apart; only female remains at nest continuously over laying period. Incubation shifts of each parent vary, from 1 to 7 days over 39–51 days incubation period. Chicks brooded continuously by either parent over first 6 weeks but may be for only 4 weeks; shifts shorter than during incubation. Chicks usually fed three times every 2 days. After guard-stage, chicks remain at or near nest while both parents feed during day. Parents return at night to feed chicks and depart at dawn; feeding shared equally by both parents (see Breeding for more details). During guard-stage many adults alternate guarding and trips to sea; after guard-stage, both parents at sea at same time and, on Campbell I. when chicks older, adults may make two trips a day (P.J. Moore). Chicks beg for food from 1–2 days old and continue until fledging. In doing so, bill vibrated rapidly against parent's belly, breast, throat or bill and utter repeated high-pitched peeping call. Adults regurgitate food directly into chick's mouth. As chick grows, it may adopt hunched or semi-prone posture to place bill lower than those of its parents. Adults reluctant to feed chicks after guard-stage, which may result in short feeding chases. Parents observed pecking at chicks after guard-stage to discourage begging. Only own chicks fed, and chicks beg only from own parents, although cross-fostering of young chicks to adults that have recently lost young has been successful. Stimulus for transition from guarding to post-guarding unknown, but probably related to increasing demands by chicks for food. Chicks gradually become more mobile after guard-stage, seeking shade under vegetation or cool damp ground near streams, and may wander seawards to meet incoming parents. Desertion of nest or loss of one adult uncommon, but may occur at any stage of breeding. Usually results in breeding failure because single parent unable to incubate eggs or feed chicks alone. However, after guard-stage, chicks have been raised by single parents. Long breeding period means that re-mating does not occur in one season. Chicks and adults will react to each other's alarm calls. Adults preen chicks from c. 1 week old to fledging.

VOICE No detailed studies and not well known; descriptions in Richdale (1951) and brief comparative analysis in Jouventin (1982); information supplied by P. Seddon. Said to be quiet (Jouventin 1982) but probably only because they do not nest colonially and thus, collectively, not as noisy as most penguins that breed colonially. Individuals utter range of loud calls: musical trills, high-pitched throbbing and harsh yells and grunts. Most calling restricted to breeding season and associated with agonistic and sexual displays; generally quiet outside breeding season but Contact Call uttered throughout year. No apparent sexual differences in vocabulary, though males use Ecstatic Display Calls much more often than females. No information on individual differences or geographical variation. Non-vocal sounds: made by flippers hitting opponents during fights and when rapidly vibrated against female's body during copulation.

ADULT Ecstatic Display Call (= Full Trumpet of Richdale 1951). Very loud, musical trilling, 'suggestive of the tremolo of giant crickets' (Richdale 1951); consists of series of repeated syllables c. 0.16 s long, each consisting of about five short (c. 0.03 s duration) notes; main frequency c. 1500 Hz, maximum frequency c. 6000 Hz; one example contained 21 syllables, initial and final syllables varying (Jouventin 1982). Sonagram A shows a phrase of 7 syllables. Most commonly given by lone males at nest and most commonly during the



A J. Kendrick; P100

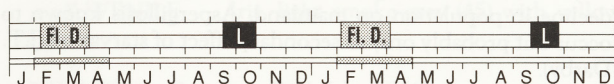
pre-egg period; most calling at dusk. Appears to function in advertising and individual recognition. **Half-trumpeting**. Closely similar to Ecstatic Display Call but less regular; described as 'half-hearted trumpets' (=Ecstatic Display Call) but with 'less of the pretty musical warbling and a preponderance of yelling' (Richdale 1951); syllables longer in Half-trumpet than Ecstatic Display Call; given as duets but with male uttering more syllables during duet. Given by mated pairs, usually at nest-site and most often during breeding season. Used as courtship display during pre-egg stage and as greeting at nest-relief during incubation and guard-stages; probably important in individual recognition. **Contact Call**. High-pitched musical two-syllable call, from which Maori name *Hoiho* comes. Given throughout year; when returning to breeding sites, given in water or soon after landing; also when alone or when returning to mate or chicks at nest; possibly also given at sea, though behaviour at sea little known. Appears to function in individual recognition and location, because mates and chicks may respond with calls or approach. **Open-yell**. Loud, piercing abrupt single note call. Given as Threat in response to sudden disturbance; also in alarm or distress (e.g. when captured) when utter prolonged repeated Open-yells. Given most often when conspecifics enter territory (though this is rare because nest-sites are isolated). **Throb**. Guttural and harsh, described as resembling series of chuckles or grunting chuckles. Appears to function as Threat Call but often given before Ecstatic Display and Half-trumpet; as threat, likely to indicate general location and excited state (and thus used before sexual displays). When given as threat, appears to signal tendency for further aggressive behaviour.

YOUNG Medium- to high-pitched *cheep*, pitch varying in different circumstances: lower when begging and as contact call; more highly pitched when distressed. Harsh rasping as threat, before attacking. Probably also functions in individual recognition.

BREEDING Well known. Major detailed studies by Richdale (1951, 1954, 1955, 1957), J.T. Darby, P. Seddon, Y. van Heezik and P.J. Moore; information contributed by last four workers. Though Richdale freely described nesting as colonial, which has been interpreted to mean that breeding behaviour depended in some respects on contact between pairs, recent work (J.T. Darby, P. Seddon, Y. van Heezik) has shown that pairs usually cannot see their neighbours and do not need to hear them. If within sight of each other, one or both pairs always fail and fewer than 1% of pairs can see each other. Thus at best regarded as loosely colonial. However, birds tend to nest in particular areas and come to land at special points, being forced to do so by the precipitous nature of coastline. Thus, there are few mainland sites that meet their requirements: only 41 on SI, ranging in size from 2 to 28 pairs, scattered in groups over large areas and only where suitable cover remains in now sparse and usually discontinuous

patches. In the Catlins, 200+ birds recorded breeding in area c. 150 ha (Richdale 1941); five pairs now survive in same area. On Campbell I., nine main breeding localities, 172 landing sites of 1–143 individuals.

SEASON Usual limits are from laying in Sept. to fledging in Feb. and Mar., occasionally to mid-Apr.; building or attendance at nests may start in May. Earliest clutch recorded 11 Sept.; latest 22 Oct. Mean date of laying of first egg 24 Sept. (5.4 days; 11 Sept.–11 Oct.; 701) (Richdale 1957). Season on Campbell I. up to 2 weeks later (Bailey & Sorensen 1962) and differences from year to year. Lack of food may have delayed laying by 6 days from the mean in 1939 (Richdale 1957) and by 10 days for 35 clutches in 1986 (J.T. Darby). Mean date of hatching on Campbell I. 26 Nov. (3.4 days; 66) (P.J. Moore). Adults at colonies throughout year; immatures arrive as early as July but mostly in late Aug. to early Sept. Young leave from late Jan. to mid-Apr.; mean date of departure 28.4 Feb. (6.8 days; 70) (J.T. Darby); on Campbell I., 13 Mar. (7.9 days; 56) (P.J. Moore). Immatures mobile; about half those in a breeding area are from outside that area; those that moult in an area tend also to breed there (Richdale 1957).



(Fl. D. Departure of fledgelings only)

SITE Historically believed to breed in coastal podocarp and hardwood forests. Nowadays in various coastal habitats on mainland and modified subantarctic islands; on coastal cliffs and up to 1.0 km inland; in *Dracophyllum* scrub and tussock on Campbell I., which never forested. Sites sheltered from elements, particularly direct sun, but some, specially those facing seawards on steep cliffs unprotected but yet sunless and cooled by sea-breezes. Secretively placed on ground, usually under dense overhead cover, inconspicuous and well-hidden. Also in crevices and on ledges on cliffs, where available; rarely in natural holes and never in caves or burrows. Often at base of large trees or alongside fallen logs. In areas of scattered shrubberies, e.g. *Phormium tenax*, rarely more than 1.5 m from periphery. Will breed in large nest-boxes placed on or near existing sites. Some sites may be used for years by same birds: five pairs nested in same site for 7 years, out of 65–120 nests followed each year; yet more than 70% of pairs followed used different sites each year (J.T. Darby). Pairs may alternate between sites from year to year and at 4–5 weeks of age chicks wander and may be found at a previous year's site (J.T. Darby). No nesting association with other species. Sites apparently chosen by either sex (Richdale 1951; J.T. Darby; P. Seddon; Y. van Heezik) but loss of one member of pair may affect the matter, which is exceedingly hard to assess because the birds are so shy and secretive. In general, sites and pairs are changed most often where nesting density is high. Disturbance by stock and man during pre-egg stage influences selection of site and pairing (J.T. Darby).

NEST, MATERIALS An open shallow bowl, often substantial, where there is plenty of material; made of twigs, grass, tussocks, leaves, plant stems. Nests in farmland more capacious than those in forest. Diameter, 50–80 cm and up to 15 cm high. Both sexes build, alone or together, when one brings material, other arranges it. Before laying, less than 3% (0.5–3.8) of time spent building in equal proportions; during incubation, average 2% (0.1–2.3) of time on building, mostly

arranging and mostly by male; during guard-stage, nest arranging for 0–0.5% of time; nest not usually used after guard-stage. Material usually collected near nest but also from up to 30 m; dropped into bowl with shake of head; arrangement of material by bird on nest reaching outside and picking up and pulling material in with shake of head. Shaping of bowl by pressing down body and occasionally scraping with feet when bird is prone. Building is part of courtship behaviour (see Social Behaviour). Lone birds liable to build or arrange material at any time of day; otherwise most building in late afternoon or early morning after or just before departure of one bird. Bulk of structure assembled during about 1 week and 4–10 days before laying but building continues for 6 weeks during incubation. Previous year's nests have usually disappeared by start of next season and so generally have to be rebuilt. Up to three building attempts may be made before choice of final site. Pilfering from neighbour's nests not recorded and unlikely because nests are so far apart and out of sight.

EGGS Oval; smooth, mat; bluish green when laid, becoming white after 24–36 h; rarely spotted or blotched at apex.

MEASUREMENTS:

76.95 (2.3; 68–83; 592) x 57.5 (1.35; 51.26–62.5) (Richdale 1957)

75.62 (2.23; 71.5–80; 26) x 57.06 (1.97; 51.8–60.7) (J.T. Darby).

WEIGHTS:

137.8 (7.75; 111–158; 446) (Richdale 1957)

128.4 (7.84; 100.65–134.8; 26; incubated 3–5 weeks, two infertile) (J.T. Darby).

CLUTCH-SIZE One or two. Females more than 2 years old almost always lay two; less than 5% of them lay one. Two-year-olds generally (75%) lay one. Single brooded. No replacement clutches.

LAYING Not closely synchronized in colonies; see above for extreme and mean dates of laying. Some geographical difference and mean date delayed in some years (see above). Time of day of laying not known. Interval between eggs 3–5 days (J.T. Darby); 2x3 days, 55x4 days, 25x5 days (n=82 clutches; Richdale 1957). Multiple laying in one nest (2xC/3, 1xC/4) recorded in only three of 800+ nests (J.T. Darby), probably because neighbouring nest-site destroyed.

INCUBATION Equally by both sexes in stints of 1–7 days; on average, females for 1.8 days (0.6; 1–7; 44), males for 2.0 days (0.7; 1–7; 44). If mate lost, may sit for 15 days (J.T. Darby). Starts soon after laying of second egg. **INCUBATION PERIOD:** 43.5 days (39–51; Richdale 1957); 42.9 days (2.2; 39–51; 41) (P. Seddon). Mean hatching date 9 Nov. (Richdale 1957). Two infertile clutches incubated for 70 and 76 days and then deserted. Both eggs hatch at about same time; of 385 two-egg clutches, 63% hatched same day, 31% one day apart, 5% two days apart and 1% three days apart (Richdale 1957). No disposal of egg-shells except usually by pushing them out of nest. When incubation starts seriously with second egg, incubation birds takes up prone position on nest for average 92.5% of time.

NESTLING Semi-altricial, nidicolous. Hatched with light to neutral grey down, slightly paler on neck, breast, belly and perhaps on back; upper side of flippers much lighter than back; below paler still and with sparse down; blind, eyes opening at 3 days. Mesoptile appears on back at 8 days. Feathers appear all over body at 43 days; visible on head at 64 days in pattern of colouring; white feathers clearly visible in patches

below but mesoptile persisting on throat and neck; flippers free of down; blue feathers plain. By 85 days, filoplumes on head gone and few traces of down elsewhere; pattern on back, well defined. By 113 days, traces of down remain only on back of head and, in general, young bird appears brilliant white in front with fresh violet-blue upperparts (Richdale 1941). **NESTLING PERIOD:** 106 days (4.9; 97–118; 85) (Richdale 1957); 103 days (5.1; 71) (J.T. Darby); 108 days (6.5; 97–119; 56) on Campbell I. (P.J. Moore). Brooded by both parents, sitting prone on young for 60% of time for first few days; for 30% of time after 14 days; for 20% after 21 days. Guard-stage gradually develops from true brooding after about 3 weeks as chicks grow too big; one or both adults stay with chicks for at least 6 weeks, depending on size of brood (one or two) and availability of food. With B/1, guard-stage may be extended for up to 4 weeks; when food scarce, may be reduced by 10 days (J.T. Darby); Richdale (1957) found no difference in length of guard-stage between B/1 and B/2. No true crèche-stage (Richdale 1957); small congregations of 3–7 chicks occasional but very rare; perhaps more common on Campbell I. where good populations; of 34 birds, 10 regularly congregated as 2–3 broods (P.J. Moore). Adult feeds only own chicks (J.T. Darby). Fed by incomplete regurgitation. If one parent dies at or near end of guard-stage, other can rear two chicks, which are usually underweight (Richdale 1957; J.T. Darby). Adults defaecate over edge of nest, as do chicks to 2 weeks old. Dead chicks not readily removed. Adults generally very timid but varying according to stage of annual cycle. Before laying they usually run away; usually approachable during egg- and guard-stages. During post-guard stage, usually run at sight of intruder but some defend chicks aggressively (P.J. Moore). No or little anti-predator behaviour by adults or young; chicks often killed close to or even under brooding parent.

GROWTH Weight at hatching: 108 g (18.5; 44) (J.T. Darby). At fledging 5.86 kg (0.73; 4.3–7.0; 73) (J.T. Darby) or 107% of average adult weight; at Campbell I., 5.1 kg (0.7; 3.0–6.2; 25) (P.J. Moore) but wide annual variation: 6.1, 5.4, 4.4 in three seasons (Y. van Heezik). Length of flipper increases (10-day intervals to 40 days; in mm) from 39 (3.8; 22), 66 (8.7; 37), 124 (14.2; 29), 187 (13.1; 22), 218 (10.0; 30) to 222 (9.2; 26) at 60 days, 229 (7.7; 32) at 80 days and 229 (6.5; 20) at 100 days. Tail measurements at about 40-days-old, 2.5; grows to 34.6 (6.6; 29) at 60 days, 62.2 (4.3; 39) at 80 days and 66.9 (3.9; 22) at 100 days. Culmen at hatching, 15.6 (0.7; 22) to 25.4 (1.7; 29) at 20 days, 38.3 (1.7; 39) at 40 days, 50.3 (1.5; 39) at 80 days and 53.6 (1.8; 23) at 100 days (Y. van Heezik).

FLEDGING TO MATURITY About 80% of chicks leave nest at 4–5 weeks old and move to new site, occasionally that of previous year's nest. Probably usually leave for sea in early morning but departures noted in late afternoon and early evening (J.T. Darby); swim immediately on reaching sea and then totally independent of parents. Mean date of fledging (departure) 28 Feb. (6.8 days; 70). First pairing by either sex at age of two years; all females have paired at 3 years of age and most males at 3–4 years (Richdale 1957; J.T. Darby).

SUCCESS Summarized below: comparison of breeding success on Campbell Island and mainland.

Birds survive for 20 years (Richdale 1957). Because habitat has been much modified, large populations of rabbits have developed in some breeding areas and this supports many predators. Major threat to chicks on mainland from feral cats, ferrets, perhaps stoats. At sea, Leopard Seals *Hydrurga leptonyx* blamed for killing birds (Richdale 1957)

References	1	2	3	4	5	6
% NESTS WITH TWO EGGS	94				97	93
% EGGS THAT HATCH	83	78	79		85	82
% EGGS THAT FLEDGE CHICKS	70		53			45
% CHICKS THAT FLEDGE	85	76	67		87	54
% NESTS THAT FLEDGE CHICKS	76		70	80		
% MEAN NO. CHICKS/NEST	1.4	1.1		1.1	1.4	0.9

References: (1) Campbell I., 1987–88, 40 nests; (2) 1936–52, 1073 nests (Richdale 1957); (3) 1970–71, 19 nests (survival of chicks up to 10 weeks old) (Roberts & Roberts 1973); (4) 1983–84, 19 nests (Lalas 1985); (5) 1981–84, 404 nests (J.T. Darby); (6) 1985–86, 622 nests (Seddon 1988).

but doubtful because these Seals are rare at Otago (only three individuals, two dying, reported in 18 years). Hooker's Sealions may take birds occasionally. Probably Barracouta *Thyrstites atum* are major marine predator, damaging legs and feet of birds and crippling them though sharks believed to take birds (J.T. Darby). Storms may have an effect by interrupting feeding (Richdale 1957). Humans have probably been, and may still be, worse menace; farming activities have destroyed much breeding habitat and have probably led to decline in population on mainland. Aspergillosis known to occur but probably only as secondary effect of starvation (J.T. Darby).

PLUMAGES

ADULT Definitive basic. **HEAD AND NECK.** Forehead and crown, cream-yellow streaked black. Feathers, cream-yellow with broad black (89) rachis, and concealed whitish bases. Broad cream-yellow eye-stripes begin at gape and meet in band across nape. Interramal region, chin and malar area, cream-yellow to straw-yellow (c56) with thin brown (119C) streaks, merging to brownish (119C, 119D) on throat and sides of neck. Hindneck, as upperparts, slate-blue. **UPPERPARTS.** Appears slate-blue. Feathers, dark grey-brown (21; mostly concealed) with light blue-grey (c88) tips and distal half of rachis. Proximal half of feather, concealed, white with dark-brown centre to rachis. Upperparts become progressively duller with wear, and in pre-moult stage, can appear dark brown. This appearance caused partly by more of bases being exposed, and partly by blue-grey tips discolouring to dark brown (c21). Amount of wear varies between individuals; wear tends to be least marked round preen gland, most marked on lower back, which can have buff-yellow tinge. **TAIL,** blackish (82); feathers have light-grey (85) edges when fresh. **FLIPPER.** Upperside, blackish, with white trailing-edge from axilla to tip; feathers with very broad rachis. Leading-edge, white from axilla to near tip. **UNDERPARTS,** white, except for small black (89) patch under posterior base of flipper. **FLIPPER.** Underside, white, sometimes with isolated black (82) feathers; has pink wash after strenuous exercise.

DOWNY YOUNG Uniform brown (light greyish 119A), slightly paler (c27) on central breast and belly. Mesoptile, slightly paler; see Richdale (1941) for details.

JUVENILE **HEAD AND NECK.** Interramal region, chin and throat, white. Centre of crown, blackish (82) streaked brown; feathers grey-brown with blackish (82) rachis and shaft-streak. Sides of crown tinged more yellow, with blackish (82) streaks; feathers, pale cream-yellow with black (82) rachis. Cream-yellow eye-stripe runs from gape to just above and behind eye. No yellow 'bridle'; this area coloured as upperparts. Otherwise, plumage as adults. Discoloration of upperparts in pre-moult stage more common and intense in

juveniles than in adults (Y. van Heezik).

ABERRANT PLUMAGES A bird without black or blue pigments collected Auckland Is (Oliver). A few birds have isolated black feathers scattered on underside (Richdale 1941; Oliver). Three isabelline birds (adult, juvenile and chick) recorded on Enderby I. in 1987 and one at Sandy Bay, Catlins, in 1983 (J.T. Darby).

BARE PARTS Based on Richdale (1941), and photos in NZRD, Harrison (1987), Peterson (1979) and unpublished (Y. van Heezik).

ADULT Iris, straw-yellow (56). Most of upper mandible, and tip of lower mandible, pale red-brown (40). Rictus, most of lower mandible, and broad patch at junction of culminicorn and latericorn, whitish to pale salmon-pink (6). Eyelids, mostly reddish pink (13), yellowish (c53) at edge. Front and sides of tarsus, and top of feet, whitish flesh (pale); after strenuous exercise flushing to startling crimson-pink (10). Soles, hind edge of tarsus and tips of webs, dark grey (83). Claws, pink-brown (brownish 5) to black-brown.

DOWNY YOUNG Full details in Richdale (1941).

JUVENILE Iris, light smoke-grey (45) with yellow tinge.

MOULTS Based on Richdale (1951).

ADULT POST-BREEDING Definitive pre-basic. Complete; full duration unknown but time spent ashore about 24 days. Moulting observed Jan.-June; most birds moult in Feb. and Mar. Early moulters are non-breeders and failed breeders. Onset of moult can be delayed to early May by food shortages; in May birds moult regardless of body condition (J.T. Darby, P. Seddon, Y. van Heezik). Normally, breeding birds moult about 22 days after young have departed. Successful females tend to moult at same time each season, males at same time as their partner.

POST-JUVENILE First pre-basic. Complete, recorded Jan.-May, but mostly Feb. and early Mar., at 14-18 months old. Timing similar to non-breeding and failed breeding adults; mean starting date 3 Mar.

MEASUREMENTS (1) Otago Pen., live breeding pairs; extended flipper from posterior axilla to tip, exposed culmen (Richdale 1951). (2) Campbell I., live breeding pairs; extended flipper from ball of humerus to tip, exposed culmen, bill depth at point of diversion of lower mandibular rami, THL from occipital condyle to bill tip, tarsus posterior length, toe to end mid-toe claw (P.J. Moore).

(3) Otago Pen., biopsied adults; methods unknown (J.T. Darby, P. Seddon, Y. van Heezik).

FLIPPER	(3) 229.1 (5.84; 115)
BILL	(3) 55.3 (1.89; 119)
BILL D	(3) 19.6 (0.89; 121)
FOOT+TOE	(3) 135.1 (4.17; 110)

WEIGHTS

ADULT BREEDING Vary considerably during year; see Richdale (1951) for details. Peak weight just before moult; minimum at end of moult. Weight rises steadily in winter to lower peak at start of pre-egg stage. In pre-egg stage, weights of males decrease and females heavier for about 4 weeks; males heavier than females at all other times of year. Weights of females decrease when first egg laid. Both sexes tend to put on weight during incubation and chick rearing, but decreases at end of guard stage, and when chicks about to leave.

OTHER AGES Little information on patterns in weight change.

Otago Pen. (J.T. Darby, P. Seddon, Y. van Heezik).

Pre-moult

Males	8.5 kg (7.3-8.9; 25)
Females	7.5 kg (6.6-8.4; 25)
Juvs	6.9 kg (5.5-8.4; 25)

Post-moult

Males	4.4 kg (3.9-4.9; 25)
Females	4.2 kg (3.6-4.8; 25)
Juvs	3.7 kg (3.1-4.5; 25)

Otago Pen., early winter (Richdale 1951; converted from lbs).

Males	5.73 kg (0.45; 4.88-6.69; 39)
Females	5.26 kg (0.44; 4.53-6.24; 39)

Otago Pen. breeding pairs, fourth week of incubation to end of guard stage (Richdale 1951).

Males	5.53 kg (0.34; 4.88-6.35; 80)
Females	5.13 kg (0.32; 4.31-5.78; 80)

Campbell I. breeding pairs, late Oct-early Nov. (P.J. Moore)

Males	5.4 kg (0.2; 5.0-5.6; 8)
Females	4.5 kg (0.3; 4.0-4.7; 7)

Mean weight loss per day while moulting: males 151 g, females 140 g, juveniles 130 g (Richdale 1957).

STRUCTURE Uncrested. Tail, short; 20 feathers. Bill long, fairly slender; upper mandible downcurved at tip. Groove between culminicorn and latericorn unfeathered. Feathering on culmen encroaches onto about one-third of bill.

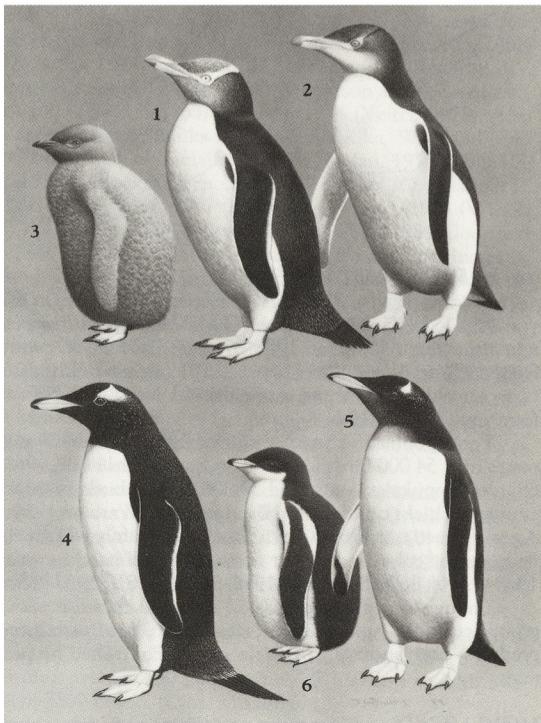
GEOGRAPHICAL VARIATION None. Large series of photos from Campbell I. (P.J. Moore) shows that these birds do not have paler face than elsewhere, as previously suggested. Triggs & Darby (1989) determined that Campbell I., Auckland I. and Stewart I.-Mainland birds are genetically discrete. DIR

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	MALES	FEMALES	
	MALES	FEMALES	
FLIPPER	(1) 215 (3.7; 207-223; 66) (2) 209 (2.5; 204-215; 39)	206 (5.1; 197-215; 70) 204 (3.2; 197-213; 39)	** **
TAIL	(1) 64.0 (4.71; 56-77; 42)	60.7 (5.42; 45-71; 47)	**
BILL	(1) 55.1 (1.52; 51.0-58.8; 66) (2) 54.4 (1.3; 51.6-56.8; 39)	53.8 (1.79; 49.3-57.8; 70) 52.8 (1.2; 50.7-55.9; 39)	** **
BILL D	(2) 20.7 (0.7; 19.2-22.7; 39)	19.4 (0.7; 18.0-20.8; 39)	**
THL	(1) 142.1 (1.90; 61) (2) 141.4 (2.4; 135.6-145.8; 39)	135.2 (1.82; 61) 136.4 (1.6; 132.5-139.8; 39)	** **
TARSUS	(2) 60.1 (1.3; 58.5-62.3; 7)	58.1 (1.2; 56.7-60.0; 7)	**
TOE	(1) 91.7 (3.56; 85-103; 66) (2) 92.2 (2.6; 83.9-95.3; 7)	86.6 (2.36; 80-92; 70) 88.1 (2.2; 86.2-92.8; 7)	** **
FOOT+TOE	(2) 134.2 (2.9; 127.4-140.2; 39)	130.4 (2.7; 125.0-135.8; 39)	**

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Yellow-eyed Penguin *Megadyptes antipodes*

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

Gentoo Penguin *Pygoscelis papua*

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

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