

Order SPHENISCIFORMES

Family SPHENISCIDAE penguins

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

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

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

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

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

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

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

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

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

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

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

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

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

REFERENCES

Kooyman, G.L. 1975. Pp 115-37. In: Stonehouse. 1975.
Rijke, R.M. 1970. *J. Exp. Biol.* 52: 469-79.

Simpson, G.G. 1975. Pp 19-41. In: Stonehouse. 1975.
Stonehouse, B. (Ed.) 1975. *The Biology of Penguins.*

Eudyptula minor Little Penguin

COLOUR PLATE FACING PAGE 241

Aptenodytes minor J.R. Forster, 1781, *Comment. Phys. Soc. R. Sci. Götting.* 3: 135, 147 — Dusky Sound, South Island, New Zealand.

Eudyptula is the diminutive of *Eudyptes*.

OTHER ENGLISH NAMES Fairy, Little Blue or Southern Blue Penguin.

POLYTYPIC Nominate *minor*, w. and se. coast SI, NZ, Stewart I.; *iredalei* Mathews, 1911, n. NI; *variabilis* Kinsky & Falla, 1976, s. NI, Cook Str.; *albosignata* Finsch, 1874, central e. coast, SI; *chathamensis* Kinsky & Falla, 1976, Chatham Is; *novaehollandiae* (Stephens, 1826) s. Aust.

FIELD IDENTIFICATION Length 40–45 cm; flipper 11–14 cm; bill 30–45 cm; weight: c. 1 kg. Smallest penguin; stocky build. Blue above, white below. Slightly hooked blackish bill. Lacks conspicuous crests or head markings of other penguins. Sexes similar but females slightly smaller. No seasonal changes in plumage. Juveniles separable.

DESCRIPTION **ADULT.** Forehead, crown and dorsal surface, indigo-blue (feathers have black shafts). Cheek and ear-coverts, dark slaty-grey, merging with white throat. Flippers, dark indigo-blue dorsally with double row of white feathers on trailing-edge, amount of white varying. Tail, indigo-blue with black feather shafts; variations include white patch on rump, upper tail-coverts or rectrices or sometimes wholly white tail. Underside, from chin to under tail-coverts, white. Underflipper, white with varying blackish patch at tip. Bill stout, slaty-black with lower edge of mandible paler; shape of bill varies; premaxilla has slight hook. Iris, light silver-grey, bluish grey or hazel. Feet, white above; back of tarsi, webs and soles, black. Claws, black. Dorsal plumage becomes darker blue as lighter feather edges wear off. Rectrices often wear down to bare shafts. Before moult some birds develop large white patches on rump round preen gland, perhaps caused by excessive feather wear during preening. Old dorsal plumage has brownish cast during moult. **FLEDGELING.** Similar to adult but smaller, with shorter, slimmer bill. Dorsal plumage lighter and brighter blue than adult. Plumage becomes duller with wear.

SIMILAR SPECIES Smaller than all other penguins but could be confused with recently fledged *Eudyptes* and *Spheniscus* penguins, particularly Rockhopper Penguins *Eudyptes chrysocome*, that have dark bills, bluish dorsal plumage and supercilary stripes inconspicuous or absent.

On land, move upright or with stooped waddle. At sea, usually show only head and small area of back above water but tail sometimes vertical. Often occur in small loose groups at sea but may form larger groups off major breeding areas before coming ashore at dusk. Breed colonially, semi-colonially or as isolated pairs. Bark-like contact call used at sea; inhalation-exhalation braying call used on land and occasionally at sea; also produce harsh growling sound when disturbed on land.

HABITAT Occur in temperate seas; within summer isotherms of 20 °C in N and 13 °C in S (Kinsky & Falla 1976). Feed mainly in inshore waters round mainland coast or breeding islands (Kinsky 1960; Reilly 1978); out to continental shelf and slopes (Reilly 1978). Often in bays, harbours, estuaries (Phillips 1961; Kinsky 1960; Milledge 1977; Pescott 1983; Dann *et al.* 1991).

Breed on coastal mainland or islands of Aust. and NZ. In Aust., mainland colonies small; often in inaccessible bays at base of cliffs (Phillips 1961; Reilly 1974; Harris & Norman 1981). Most colonies on sandy or rocky islands; on shores, coastal slopes, promontories, bases of cliffs, central flats and plateaux, sand dunes (Phillips 1961; Eckert 1971; Harris & Deerson 1980; White 1981; Brothers 1983; Lashmar 1987). Some nesting islands small and lower levels exposed to storm-waves and spray (Lashmar 1987). NZ nesting habitat similar to that in Aust. (Guthrie-Smith 1914; O'Brien 1940; Richdale 1940; Kinsky 1960; Meredith 1984; Cunningham & Moors 1985).

Prefer sandy beaches for landing (Warham 1958) but also use rocky shores and able to jump onto rock ledges from swell (Pescott 1965). Moult under shelter of rocks or bushes or in

burrows, favouring sites close to sea (Warham 1958). Mean maximum diving depth 30 m (9–69; 32; Montague 1985).

Wherever human habitation has altered breeding areas, populations have declined or disappeared (Aust. Atlas). Colonies adjoining housing developments or farmland may suffer loss or alteration of habitat by grazing, trampling, invasion of weeds, increased erosion and water run-off (Harris & Bode 1981; Harris & Norman 1981). If rabbits eliminated from islands, vegetation can recover from grazing (McManus 1979). Effects of changing freshwater discharge into sea should be examined, as may change distribution of prey (Harris & Norman 1981).

DISTRIBUTION AND POPULATION S. Aust., round NZ mainland and offshore islands and Chatham Is. Breed mostly on offshore islands, occasionally on mainland at isolated sites.

AUST. **Qld:** only rarely reported: Mooloolabah, Coolangatta and Moreton Bay (HASB). **NSW:** increasingly frequent southwards along coast; few reports N of Port Stephens (Aust. Atlas). **Vic., Tas.:** common along coast and islands. **SA:** common but rarely reported in head of Bight, which may reflect lack of observers as breeding occurs at foot of Nullarbor cliffs (Reilly 1974); many recoveries of Penguins between Victor Harbour and Port MacDonnell (Dann *et al.* 1991). **WA:** coast and islands from Eyre to S of Fremantle (HASB).

NZ N from Taranaki to Hawke Bay and offshore islands; central NZ from Hawke Bay to Kaikoura on E and Cape Egmont to Punakaiki on W including coast and islands of Cook Str.; e. coast from Gisborne to Southland; in SI, from Oamaru to Stewart I. and N to Golden Bay; straggler to Snares Is. **NI:** frequently observed along coast and islands from Auckland to North Cape and S to Coromandel Pen., then

sparsely reported through Bay of Plenty to Hawke Bay (Napier), including Mayor and White Is, then only near Wellington, Kapiti I. and near Mokau. **SI:** common from Wekakura Point through islands of Cook Str. to near Blenheim, then isolated records at Kaikoura Pen., near Scargill, round Banks Pen., Hakatere (Canterbury Bight), Otago Pen. and Dunedin, near Owaka and Bluff, fairly common between Puysegur Pt and Doubtful Sound, irregularly from Cascade Pt to Abut Head, then common near Greymouth (NZ Atlas). Chatham Is: Main, South East and Big Mangere Is (Kinsky & Falla 1976; NZCL; NZ Atlas).

BREEDING Known Aust. breeding sites (from *Corolla* Seabird Is Ser., Aust. Atlas and Aust. NRS, unless indicated):

NSW:

N. coast, se. Newcastle: S. Solitary I., Delicate Nobby I., Statis Rock, Broughton I., Cabbage Tree I., Boondelbah I. Largest population (as estimated 1960–1977) on Cabbage Tree and Boondelbah Is, elsewhere few pairs. Total numbers 2000+ pairs.

Central coast, Newcastle–Wollongong: Moon, Bird, Lion, Five Is (Flinders, Bass, Big, Martin Is). Numbers mostly small (<300), except 1000+ at Big I. estimated 1959–76. Total, c. 1500.

S. coast, Wollongong–Vic. border: Bowen I. (ACT), Brush, Berowa, Grasshopper, Wasp, Tollgate and Montagu Is. Mostly in large colonies (1000–10 000 pairs) estimated 1970–76. Total 10 000–20 000 pairs. Probably a few birds nest on rocky headlands at Burrewarra Pt (S. Marchant). A few pairs nested on mainland in Twofold Bay, Eden (Barton 1978), 25 pairs in 1982 (P. Dann).

VIC.:

E. Gippsland: Gabo and Tullaberga Is, The Skerries. Total population 5000–10 000 pairs, surveys 1972–79.





Wilson's Prom. area: Seal Is (Seal, Notch, Clifty, Rag Is), Rabbit I., Rabbit Rock, Rodondo I., Wattle I., Anser Grp (Anser, Kanowna), Glennie Grp (Great Glennie, Citadel, Dannevig, McHugh Is), Norman and Shellback Is. Total population probably 5000–10 000 pairs; largest numbers on Wattle and McHugh Is; probably extinct on Clifty I. since 1959 (Gillham 1961; Harris & Deerson 1980).

Western Port–Port Phillip Bay: Phillip I., once on nw. French I., St Kilda Breakwater (D.W. Eades), S. Channel Fort I., Middle, Merri and Mud Is. Total population >6000 pairs, surveyed in 1978, almost all on Summerland Pen., Phillip I.

W. district: Lady Julia Percy I., near Port Campbell (Reilly 1974), Griffiths I. (probably destroyed since 1971; Bowker 1980), Lawrence Rocks, Portland Harbour, Middle I. (Warrnambool). Total population c. 2000 pairs. (References in Seabird Is Ser. in *Corella* 4; Harris & Norman 1981; Harris & Bode 1981; Norman *et al.* 1980; Reilly 1977; Reilly & Cullen 1981).

TAS:

Bass Str. islands: Hogan Grp, Kent Grp (Deal, Erith, North-east Is), Furneaux Grp (Babel, Cat, Battery, Goose, Chalky, Fisher, Billy Goat Reefs, Little Green, Briggs, Great Dog, Little Dog and other islands). Not fully surveyed: population of several thousands (5000+).

E. coast, S–South-East C.: on many suitable islands throughout, even on mainland (e.g. Hobart waterfront). Mostly in modest numbers (hundreds or fewer); largest concentrations (15 000 pairs) probably on St Helens I.

S. coast (South-East C.–Pt Davey): Ile du Golfe, De Witt, Flat Witch, Walker, Maatsuyker, Louisa, Flat and Trumpeter Is. Population about 8000 pairs, surveyed by various observers between 1971 and 1981.

N. coast and King I.: Trefoil, Albatross, Walker Is, The Nut (Stanley), Doctor's Rock (Wynyard I.), Three Hummock I.; on mainland at Somerset, Three Sisters I. (Ulverstone), Wright and Egg Is, Horseshoe Reef and Wilsons Pt (Devonport), Ninth, Watchhouse, King I. (Catarqui Pt [2000 pairs], Grassy [500 pairs], Christmas and New Year Is). No recent estimates of numbers except 'hundreds' at Albatross I. (Green 1973) and 10–30 at Horseshoe Reef (van Tets 1977).

Details for some Tas. breeding colonies as result of observations between 1958 and 1983, in Seabird Is Ser. of *Corella* (Vols 1, 3, 4, 5, 7, 8, 11, 12), but for others, apparently no recent surveys.

SA:

Vic. border–Encounter Bay: C. Northumberland, C. Martin (c. 6 km N), Penguin I. (Beachport), Baudin Rocks (Robe), Granite, West, Wright Is (Victor Harbour).

Kangaroo I.: C. Coutts, Antechamber Bay, C. Willoughby,

Rocky R. (Maupertuis Bay), Breakneck R., Ravine de Casoars, Harvey's Return, Stokes Bay, Beatrice I. (Kingscote Spit), American R., Penneshaw.

Gulf St Vincent–Spencer Gulf: Troubridge I., Althorpe I., islands in Pandalowie Bay, Wedge, Gambier, Little Goose, Goose, Wardang Is, Lipson Cove (Round I.), Sir Joseph Banks Grp, Dangerous Reef, N. and S. Neptune Is.

C. Catastrophe–WA border: Greenly I., Coffin Bay (Rabbit I., The Brothers, Garden I.), Investigator Grp (Dorothee, Pearson Is), Franklin Is. Little precise data for any SA colonies by recent observations. Data mostly from Parker *et al.* (1979); see also *Corella* 1, 8 and 11.

WA:

Recherche Arch.: Six Mile, Bellinger, Lorraine, Inshore, Ben, Forrest, Mondrain, Ram, Hood, Woody, MacKenzie, Sandy Hook, Remark, Cull, Charnley, Observatory, Figure of Eight Is. References in Seabird Is Ser. in *Corella* 2, 5, 6, 8, 11, 12 for records between 1976 and 1987, which show breeding widespread in small numbers (max c. 50 pairs on Ben I.). Probably breed in most other islands; HASB records without substantiation the following as breeding localities: Boxer, Christmas, Combe, Goose, Marts, N. Turin Peaks, Rabbit, Rob, Round, Station, Termination, Wedge Is, which have not been visited recently.

Esperance–Albany: Bald, Coffin Is, King George Sound (Michaelmas, Breaksea, Mistaken, Seal Is), Eclipse I. Total population perhaps only 1000–1500 pairs. References in *Corella* 2, 5. HASB give Doubtful, Cheyne Is in addition.

Albany–C. Leeuwin: Stanley, Flat, St Alouarn Is (*Corella* 2, 8).

N. of C. Leeuwin: Safety Bay (Penguin, Shag, Seal and Bird Is), Carnac I.

NZ Known colonies include:

NI:

Northland: Twilight Bay; Parengarenga Harbour; Rarawa; Rangaunu Bay (Moturoa, Sugarloaf, & Whale Is); Simmond's Is (Rat & Kowhai Is, Shag Rock); Doubtless Bay; Cavalli Is; Moturoa I. (Bay of Islands); Hokianga Harbour, N. Head; Waipoua coast; Whangarei Harbour, n. shoreline; Poor Knights Is; Hen and Chicken Is (Big, Middle, Eastern, & Coppermine Is); Poutu.

Auckland: Mokohinau Is; Great Barrier I.; Little Barrier I.; Tiritiri Matangi I.; Noises Is; off Waiheke I.; White's Beach.

South Auckland: Coromandel; Waikawau.

Bay of Plenty: Mercury Is (Stanley, Green, Double, Great Mercury, Red Mercury & Rabbit Is); Alderman Is; Rurima Is; other islands in Bay.

Gisborne: Pourewa I. & adjacent mainland.

Wellington: Evans Bay; Somes I.; Mana I.; Kapiti I.

Wanganui: Wanganui R. estuary.

SI:

Marlborough: D'Urville I.; Titirangi Bay; The Brothers; Maud I.; Pelorus Sound, islands.

Canterbury: Motanau I.; Onewe Pen.; Banks Pen., Little Fishermans Bay; Ashburton beach.

Otago: Oamaru; Cape Wanbrow; Tuhawaiki I.

Southland: Stewart I., Ackers Pt; Codfish I.

West Coast: Taumaka I.; Charleston; Twelve Mile Bluff.

CHATHAMIS: Pinnacles; Mangere I.; Pitt I.; South East Is; Star Keys.

Counts or even estimates of breeding numbers difficult. Thus, estimates above very rough and fluctuate widely when made by different observers in different years (e.g. Phillip I.;

Harris & Bode 1981). Total Aust. population probably less than 1×10^6 and regarded as stable in spite of considerable disturbance and predation but not clear if these have significant effect on population. Birds used for crayfish bait (Bowker 1980; Warham 1979), caught in fishing nets (Robertson & Bell 1984) and otherwise taken illegally (Harris *et al.* 1980); residential development (Harris & Bode 1981) and some other human activities disturb birds and destroy nests (Harris *et al.* 1980; Harris & Bode 1981; Dann 1991). Introduced predators (foxes, dogs, cats) take adults and young and cattle trample burrows (Reilly 1977). Oil pollution kills birds (Harris & Bode 1981; Robertson & Bell 1984), plastic pollution has been responsible for deaths (Dann 1991) and fire may destroy breeding colonies (White 1979).

MOVEMENTS Adults largely sedentary, immatures dispersive.

NON-BREEDING Adults present at colonies throughout year (Kinsky 1959; Reilly & Cullen 1981) though numbers lowest between completion of moult in Apr. and start of breeding in Aug. with a three-week cycle of attendance (Reilly & Cullen 1981) although at Phillip I., each year numbers increase in May to 50% of maximum numbers. Young birds disperse widely after fledging, the direction varying with place of origin (Reilly & Cullen 1982). Most young birds return to moult at natal colonies after 3 years, some at 2 years, a few may moult and breed at other colonies (Reilly & Cullen 1982; Dann 1991). Apparent dispersal along coast possibly biased by recoveries of beachcast birds though radiotracking of adults has produced similar pattern of movement to that inferred from band recoveries (Weavers 1987; Dann *et al.* 1991). General direction of dispersal: W from Phillip I.; S from Five Is, NSW; E from Troubridge I., SA; N and S from Furneaux Grp, Bass Str., and from Cook Str., NZ; N from Hauraki Gulf, NZ (see Banding). Scarcity of recoveries of live birds in 2 years after fledging suggests they are usually at sea and could travel far offshore. Breeding adults from Phillip I. move into Port Phillip Bay during winter and early spring; first-year birds in waters off e. SA and w. Vic. (Dann *et al.* 1991).

BREEDING During breeding season, adults generally close to colony. Seen diving repeatedly within a kilometre of shore, apparently foraging (Montague & Cullen 1988) but, when absent from colonies for 2–3 days, probably travel much farther (Reilly & Cullen 1982) and birds of unknown age and breeding status seen several kilometres from coast during breeding season (Montague 1982). Likely travelling speed 0.7 m/s (Baudinette & Gill 1985; Dann & Cullen 1989) giving estimated maximum daily foraging range of 14 km in June, 20 km in Jan. (Dann & Cullen 1989).

BANDING Returns from Five Is summarized Fig. 1; from Phillip I., Fig. 2; from Furneaux Grp, Fig. 3; from Troubridge I., Fig. 4 (all ABBBS); from Hauraki Gulf, Fig. 5; from e. SI, NZ, Fig. 6 (NZNBS). Of 278 recoveries of first-year birds away from Phillip I., 4% in Port Phillip Bay; of 122 recoveries of birds >2 years old, 65% in Port Phillip Bay, one travelling minimum 47 km/day for 8 days (Dann *et al.* 1991). Smaller numbers banded Chalky I., Bass Str. and Bruny I., s. Tas. also recovered near C. Otway; recoveries of birds banded Warrnambool, Port Campbell and Gabo I., Vic., less concentrated, with young birds dispersing along coast in both directions (Reilly & Cullen 1981). In NZ, 11 distant returns from six sites around Cook Str., all <280 km, 83% to N (NZNBS). Other records (all ABBBS):

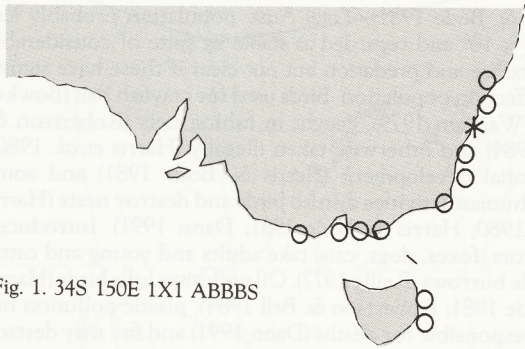


Fig. 1. 34S 150E 1X1 ABBBS

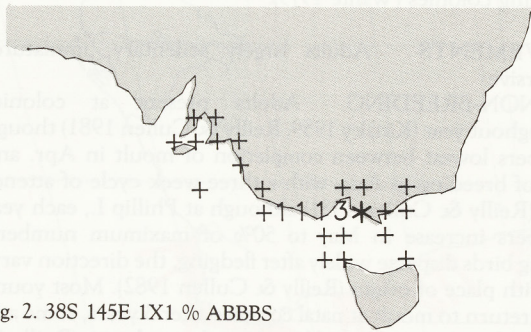


Fig. 2. 38S 145E 1X1 % ABBBS

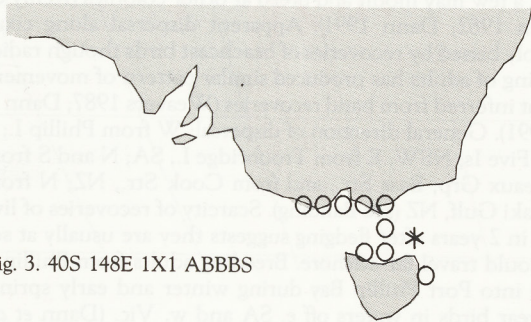


Fig. 3. 40S 148E 1X1 ABBBS

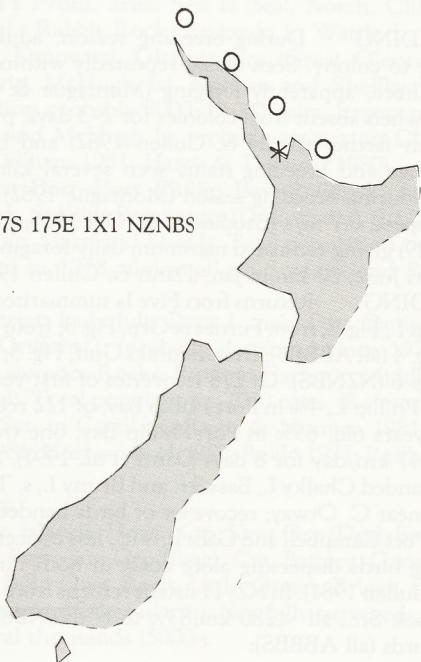


Fig. 5. 37S 175E 1X1 NZNBS

Fig. 6. 43S 172E 1X1 NZNBS



Fig. 4. 35S 137E 1X1 ABBBS

32S115E 06 1+ U 6 255 176
 32S115E 06 1+ U 24 240 180
 32S115E 06 1+ U 26 184 200

FOOD Usually small shoaling fish or cephalopods, less often crustaceans. **BEHAVIOUR.** Prey caught by pursuit-diving using wings for propulsion and tail for guidance (Carter 1910). After Penguin sights school, swims round it in diminishing circle and then plunges through middle, grabbing at fish as it goes (Dove 1910; Roberts 1951; Oliver). Schulz (1987) recognized four methods of capturing fish: (1) while circling school, snatches at breakaway fish (43% success; n=7); (2) after circling school (5.7 ± 1.13 times; n=32) swims through bunched school snatching at fish (65%; n=19); (3) after swimming through school, pursues individuals or groups for up to 5 m (50%; n=8); (4) in water <40 cm deep, pursues fish in direct line without circling (61%; n=18). Even in deeper water fish approached from side. Usually feed singly and successful manoeuvre captures a single fish, swallowed underwater (Schulz 1987). Mean depth of dive 30 m (9–69 m; 32; Montague 1985) and sprint speeds measured at 1.5–2.1 m/s (Barton 1979; Clark & Bemis 1979; Dann & Cullen 1989; Costa *et al.* 1986); measurement of 4.6 m/s by Norris (1965) probably excessive. Diving depth possibly small because anaerobic capacity of swimming muscles low (Mill & Baldwin 1983) though can remain submerged for over a minute (Barton 1979). During travelling periods to and from colony, mean dive time was

3.6 ± 0.4 s with maximum of 65 s (Costa *et al.* 1986). Most birds forage at sea from dawn to one hour before dusk. May be discouraged by rough weather (Baudinette *et al.* 1986) but dietary studies found no correlations between weight of food brought ashore and meteorological variables (Montague & Cullen 1988). Irregular availability of food used to explain low basal metabolic rate (0.6 ± 0.018 l O₂/kg.h; n=15) compared with other birds (Baudinette *et al.* 1986). Does not appear to drink sea water (Costa *et al.* 1986) but can concentrate Na⁺ to 500 mM in nasal salt glands (Baudinette *et al.* 1986).

BREEDING, NON-BREEDING At Phillip I., Vic. (770 regurgitations; Montague & Cullen 1988) fish 98.8% freq., cephalopods 34.4, crustaceans 2.2. Fish mostly *Engraulis australis* 60.8% freq., 5.49 cm (3.39; 1.0–13.0; 106; mode 3.0 cm) and *Sardinops neopilchardus* 5.14, 6.56 cm (2.79; 2.5–13.0; 86; mode 5.5 cm) with some unident. Clupeidae 0.5, *Galaxias* 0.6, *Pseudophycis bachus* 8.3, *Hemirhamphus melanochir* 1.3, Atherinidae 1.4, *Hippocampus* 0.6, unident. Sygnathidae 0.3, *Acanthopegasus lancifer* 0.1, Triglidae 2.3, Platycephalidae 0.1, *Trachurus novaehollandiae* 1.3, *Arripis trutta* 0.1, *Parapriacanthus elongatus* 0.4, *Thryxites atun* 9.0, Labridae 0.3, Blennidae 0.1, Aluteridae 10.9, Tetraodontidae 0.1, unident. 3.5. Cephalopods were *Loliolus noctiluca* 2.6% freq., *Sepioteuthis australis* 1.4, *Nototodarus gouldi* 24.8, 4.40 cm (20.3; 1–10; 65), *Argonauta nodosa* 7.5, Octopodidae 0.5; crustaceans were *Nyctiphanes australis* 1.2 (usually taken while catching *L. atun* but subsequent studies have found them important at Phillip I. in winter) and shrimp larv. 1.0. Estimates of relative quantities of fish in diet suggest *E. australis* about twice as important by weight as *S. neopilchardus*. *E. australis* eaten most frequently Feb.–June, frequency Oct.–Dec. varying between years; *S. neopilchardus* highest frequency Aug.–Nov., greatest variation Dec., Feb., Mar.; *N. gouldi* about equally frequent throughout year, greatest variability Nov.–Dec., Apr.–June; other fish species most frequent Aug.–Dec. in years when *S. neopilchardus* scarce.

At Penguin I., WA, diet almost entirely fish (Klomp 1987). *Hyperlophus vittatus* taken throughout year, *Sardinops neopilchardus* and *Hyporhamphus melanochir* mostly in autumn and winter and *Spratelloides robustus* in spring-summer, these four species making up 96% of diet by number. Also recorded taking Atherinidae (Schulz 1987).

INTAKE Average dry weight regurgitated samples Phillip I. (incl. zeros) 15.0 g (0–81; 813), weight of food regurgitated lowest June–Aug. and percentage failing to regurgitate highest June–Aug. but food taken at this time may have been caught farther offshore and digested before return (Montague & Cullen 1988). Estimated daily food intake of breeding adults during 1984, year with poor breeding performance, 167 g pilchards and anchovies/kg/day (Costa *et al.* 1986).

SOCIAL ORGANIZATION Based mainly on Waas (1988a,b, 1990), Reilly & Cullen (1981), Montague (1982) and Dann & Cullen (1990). Information supplied by P. Dann. In pairs within colony throughout much of year; in small groups or solitary at sea. Details of flocks not known but young birds from Phillip I. have different range in non-breeding season from that of adults. Therefore, age composition of flocks will vary between these areas. After feeding, form tight groups offshore from breeding colony until dusk. These groups break up into smaller ones as birds move towards shore and across beach. Once away from beach-front, groups disperse into territorial pairs within colony.

BONDS Sustained or long-term monogamous.

Likelihood of divorce 18% p.a.; length of pair-bond does not influence probability of separation (Reilly & Cullen 1981). Sex-ratio, age at first pairing, unknown, though half the individuals were known to breed for first time when 2 years old and the other half at 3 years (Dann & Cullen 1990). Separations may occur soon after previous season ends or up to the month before next season begins (Reilly & Cullen 1981). Both parents incubate and tend young until fledging. Up to eight individuals from four adjacent broods found sharing same burrow during later stages of chick development. Small crèches of 3–6 birds common in cave colonies (Waas 1990) but not elsewhere.

BREEDING DISPERSION Colonial. On Phillip I., mean nest density 4.1/m² (3.8; 0.6–14.6). Pairs form territory round burrow in breeding season; distance between nests rarely closer than 2 m, usually between 5 and 10 m. Burrow used throughout year; visited occasionally during non-breeding period, sometimes used for moulting. After feeding at sea and preening close to shore upon arrival at colony, most activities performed near burrow. Young sometimes travel considerable distance from burrow to meet parents returning from sea.

ROOSTING Generally solitary or in pairs when loafing or sleeping; in burrows if ashore during day, or on ground surface and in burrows at night. Roosting activity at sea unknown. Roosts usually unconcealed, but often protected from prevailing wind; usually in territory but sometimes outside. Some individuals use same roosts regularly; others do not. First birds leave sea at dusk, but some continue to arrive at colony for up to 2 hours afterwards. Leave colony in hour before dawn.

SOCIAL BEHAVIOUR Details of social behaviour becoming well known. Based mainly on observations in NZ (Kinsky 1960; Waas 1988a,b), Tas. (Warham 1958), WA (Montague 1982) and review by Jouventin (1982).

Usually active outside burrow only at night. Social interactions observed in artificial burrows (Warham 1958; Reilly & Balmford 1975; Waas in press) or in caves (Waas 1990, in press). However, night-vision aids or birds accustomed to artificial lighting (e.g. at Penguin Parade, Phillip I., Vic.) required. Little known of behaviour at sea. Display conspicuous because usually accompanied by calls; most nocturnal of all penguins; have surprisingly diverse array of visual displays (Waas 1988b, 1990, in press). Contact calls appear to function in promoting social cohesion, but other unknown factors probably also integrate members of flocks.

AGONISTIC BEHAVIOUR Waas (in press) grouped aggressive behaviours of both burrow- and cave-dwelling birds into Offensive Stationary Behaviours, Distance Reducing Behaviour, Contact Behaviours and Overt Aggression. **THREAT. Offensive Stationary Behaviours.** These behaviours typically accompanied by calls (see Voice) and usually performed when opponent over 1–2 m away. Offensive Stationary Behaviours used by cave-dwellers: **Direct Look:** in upright posture, bird turns body and bill towards opponent. Sometimes erects feathers on crown and round eyes. Growl call (see Voice) occasionally used. **Point:** body and head held low with neck outstretched; bill pointed directly towards opponent. Flippers sometimes held upward, away from body. Growl call often used. **Directed Flipper Spread:** body held upright, flippers outstretched. Sometimes erects feathers on crown and round eyes. Bill and white underparts directed towards opponent while bird Growls or Brays. **Bowed Flip-**

per Spread: similar to Directed Flipper Spread, but bill directed downward into nest-bowl or territory as bird walks in tight circles round nest. Sometimes erects feathers on crown and round eyes. **Directed Mutual Display and Bowed Mutual Display:** very similar to Directed Flipper Display and Bowed Flipper Spread respectively, but performed in unison by both members of mated pair. One member usually vibrates flipper on partner's back. Both displays usually accompanied by Braying call. Mated pairs perform **Upward Mutual Display:** hold bodies and bills straight upward and flippers outstretched while Braying. Members of pair usually within 0.5 m of each other. Typically occurs after series of intrusions by neighbouring birds or strangers. Offensive Stationary Behaviours used by burrow-dwellers: **Stretch-neck Look:** bird inside burrow stretches neck so that head protrudes from entrance; then looks toward intruder. Sometimes erects feathers round eye and on crown. Growl call occasionally used. Stretch-neck Look roughly equivalent to Direct Look of cave-dwellers. **Bill Vibe:** bird inside burrow directs lowered head towards entrance and vibrates bill from side to side while Growling. Bill Vibe roughly equivalent to Point of cave-dwellers. Burrow-dwellers also use Directed Flipper Spread, Bowed Flipper Spread, Directed Mutual Display and Bowed Mutual Display very similar or identical to those of cave-dwellers. **Distance Reducing Behaviour:** usually initiated when opponent 1-2 m away, and commonly accompanied by calls. Distance Reducing Behaviours used by cave-dwellers: **Zig-zag Approach:** body and head held low to ground (similar to posture used in Point); bird approaches opponent obliquely in zig-zag manner, turning every few steps. Growl call sometimes used. **Directed Flipper Spread Approach:** bird adopts same posture as for Directed Flipper Spread and walks directly and rapidly towards opponent. Growl or Bray calls sometimes used. **Direct Mutual Approach:** Directed Flipper Spread Approach performed by mated pairs in unison. One member of pair usually vibrates flipper on partner's back. Always accompanied by Braying. Burrow-dwellers use only one Distance Reducing Behaviour: **Lunge-hiss:** bird inside burrow throws itself towards entrance with outstretched flippers; as bill reaches outside entrance, bird Hisses or utters Aggressive Bark, then springs back into burrow by pushing flippers against entrance walls. **FIGHTING. Contact Behaviours:** typically silent and brief. Contact Behaviours used by cave-dwellers: **Bill to Bill:** opponents reach towards each other with closed bills and touch bill-tips; may bob heads up and down and raise and lower flippers. **Bill Slapping:** sometimes follows Bill to Bill. Opponents knock each other's bills from side to side while raising flippers. **Breast Butt:** bird pushes breast several times lightly against opponent, to direct it away from defended area. **Bill to Back:** bill lightly placed onto opponent's back after it has turned away. Bird may follow opponent as it moves off, holding bill against its back until well outside defended area. **Bill Lock Twist:** opponents interlock bills and twist from side to side; flippers usually extended and birds utter Growls and Aggressive Yells. Burrow-dwellers use one Contact Behaviour: **Lunge Peck:** bird launches itself out of burrow, so that bill touches opponent; then freezes, pointing bill towards opponent. **Overt Aggression:** if intruder does not retreat, defending birds may attack. Cave- and burrow-dwellers fight in two ways; may use Growl, Aggressive Yell and Aggressive Bark during fights. **Bite Nape Fight:** bird bites and holds opponent's nape and twists skin while bashing opponent's sides and head with rapid flipper blows. Opponent usually swings

head back and from side to side, attempting to bite attacker's flippers or sides. **Bill Lock Fight:** opponents inter-lock bills and bash each other with flipper blows to sides. Each attempts to throw other off balance by twisting from side to side. **APPEASEMENT. Defensive Stationary Behaviours** (Waas in press): bird turns head and body away from opponent; silent. Cave-dwellers use 2 Defensive Stationary Behaviours. **Indirect Look:** bird turns body slightly away from opponent; raises head to one side and looks at opponent with one eye. Bill sometimes pointed up and away from opponent. **Face Away:** body turned directly away from opponent; head may be turned slightly so that bird can glance back. Burrow-dwellers use Face Away, usually at rear of burrow, but apparently not Indirect Look. **ESCAPE. Distance Increasing Behaviours** (Waas in press): used to avoid opponent's approach or to escape dangerous interactions; silent. Cave-dwellers use 2 Distance Increasing Behaviours. **Submissive Hunch:** bird turns directly away from opponent, extends neck so that head held as far away from opponent as possible, and takes 2-3 steps away before stopping to look back. **Low Walk:** body and head held low and flippers held close to sides as bird walks or runs away from opponent. Used when moving through defended areas, passing other penguins, or escaping agonistic interactions. Burrow-dwellers use Low Walk but apparently not Submissive Hunch. Differences in habitat do not affect manner of Low Walk.

SEXUAL BEHAVIOUR ADVERTISING DISPLAY (Solo Call of Waas [1988b]). Similar to some Threat Displays, particularly Directed Flipper Spread and Bowed Flipper Spread, but bill usually pointed straight upward and flippers may be held much higher above back; always accompanied by Braying call. Typically performed outside nesting areas by unmated males to attract unmated females (Waas 1988b); but may also be performed by mated males or females on or near nest-site, which suggests dual function in mate-attraction or maintenance of territory; may also help members of pair to locate each other when separated by disturbance (J.R. Waas). Mainly used in breeding season and few months before, but may occur at any time of year; used least during moult and immediately after breeding. Used more often in first two hours after dusk and in last two hours before dawn. At Phillip I. (Vic.), males may dig burrows before pairing, and display in front of them for mates (P. Dann); but, on Banks Pen. and Motunau I. (NZ), burrow-dwelling males advertise along rocky shorelines below nesting areas and search for nest-sites only after pairing (Waas 1990). In colonies in caves, unmated males occupy central neutral areas without nest-sites and advertise for females; frequently form small calling-clubs of 3-6 males (Waas 1990, in press). After pairing, birds move into nesting areas to search for suitable sites. **COURTSHIP. Sexual Mutual Display:** initiated by either bird standing erect, spreading flippers and bowing head (J.R. Waas). Partner copies behaviour and both birds may walk in tight circles round nest-site. Male sometimes vibrates one flipper on female's back as they move. Both birds call simultaneously with Braying call. Used in courtship, nest-relief, and perhaps mate recognition; always precedes copulation. No courtship feeding recorded. **ALLOPRENING.** Non-ritualized; of head and neck; may be simultaneous or reciprocal; usually seen after bird arrives in colony in breeding season and relieves mate at nest or at any time of year between birds on tracks leading from beach. **COPULATION.** Occurs inside or close to burrow and usually follows Sexual Mutual Display. As intensity of Sexual Mutual Display increases, male moves alongside female

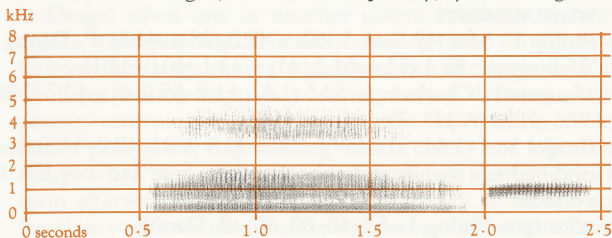
and makes contact with bill and flippers; female lies on ground, male mounts from side and climbs on her back. Male beats flanks of female with flippers, producing drumming sound, while he vibrates bill round her face or bill. Appears to be no post-copulatory display. Duration of copulation few seconds to few minutes; occurs often and has been recorded up to nine times in 2.5 h for one pair (P. Dann). Copulation obvious because male makes drumming sounds; most frequent during months before breeding and early parts of breeding season and far less common during chick-rearing period.

RELATIONS WITHIN FAMILY GROUP Both sexes observed digging burrow and building nest, but males do most work. Incubation shared equally by sexes and shifts vary widely, depending on feeding conditions and perhaps individual differences. Both parents share in brooding and guarding of young. In first few days after hatching one parent remains with young continuously while other feeds at sea; at this stage, change-overs occur daily. After c. 2 weeks, both parents go to sea each day and return in evening; adults may not return for several days. Although eggs may sometimes be deserted, no evidence that desertion of young occurs. Young actively beg for food by calling and, as they become older, pursue parents relentlessly; their persistence usually drives parents some distance from burrow after young are fed. Food is transferred directly from parent to young by incomplete regurgitation. Aggression between young and parents seen only occasionally when fully fledged young driven from natal burrow. Adults aggressive towards young of others when approached for food; suggests that adults can recognize own young, but appears less likely that young can recognize own parents. Visual means of communication between adults and young not known. Young independent of parents after fledging; adults and young migrate to different areas after breeding season (see Movements).

VOICE Only quantitative studies by Jouventin (1982) and Montague (1982). Waas (in press) provides sonagrams of agonistic calls. Generally noisy on land at night; call intermittently at sea. Calls vary from short yaps and harsh grunts to long, loud pulsed trilling and braying. Three fundamental vocalizations: contact and agonistic calls and display songs of single birds or pairs (Jouventin 1982). Montague (1982) identified eight categories, including one probably non-vocal sound made before copulation. Waas (1988b) identified 5 types of agonistic calls. No mimicry. Calling most frequent after dusk when birds have returned from sea and again before pre-dawn departure. Calling frequency at sea unknown. Calls may be heard throughout year but more frequent in months before and during breeding. All social calls, except contact call, generally made near burrow. Quality of calls similar between sexes; no significant differences between male and female calls for length, maximum frequency, syllable length or

sideband interval. However, main frequency of male calls recorded at Phillip I. higher than that of females (Burger 1987). Vocabulary of sexes similar but females probably less vocal during advertisements, attraction and threat displays (Montague 1982). Warham (1958) noted that contact calls of males deeper than those of females. Duetting occurs during sexual and agonistic Mutual Displays. Hodgson (1975) believed that individual differences could be recognized. Rhythm of advertisement song differs between individuals (Jouventin 1982). Main frequencies of songs of both sexes vary (Burger 1987). Subspecific variations have not been examined. No communication with young recorded. No calling during copulation recorded.

ADULT (1) **Advertising Call: Braying** call consisting of extended exhalant throbbing followed by shorter inhalant squealing sound described as a 'whoop' by Warham (1958) (sonagram A). Representations include: *urrrrrrrrrrr . . . urrrrrrrrrrraaaaawoooo . . . rrrr . . . aaaaowooo . . . raowoo* (Hodgson 1975). Described in its various forms as 'Half-trumpet', 'Full-trumpet' (Warham 1958; Hodgson 1975), 'whole ecstatic display song' (Jouventin 1982) and 'Solo Call' (Waas 1988b). Varies in complexity; variations associated with changes in posture. Often used by lone, apparently unmated, males at entrance to burrows. At Penguin I., WA, rate of calling in July increased from dusk to secondary peak just before midnight; main peak before dawn (Montague 1982). Sharp increase in use before and during early stages of breeding. (2) **Courtship Call**: similar to Advertising Call but posture of caller different, phrasing of call and length of call may be shorter. Commonly begins as low-pitched expired throbbing (**Growl**), which may develop into, or come from, **Braying**; Hodgson (1975) described throbbing element phonetically as *urrrrrrrrrr*. Often precedes copulation or follows aggression with third individual. Playback of Advertising and Courtship Calls significantly increased frequency of performance of Courtship Displays and copulation (Waas 1988b). (3) **Greeting Call** similar to elements of Advertising Call and identical to Courtship Calls except often in duet and accompanied by Mutual Displays. Birds calling during duets are nearly always out of phase with each other (Montague 1982). (4) **Agonistic Calls** (Waas 1988b). Low throbbing **Growl** *urrrrrrrrrr* produced as bird exhales (Hodgson 1975), varying much in length and volume and similar to many Courtship Calls. Uttered in response to noise of passing mammals or conspecifics; entry of other individuals into their burrows; or Advertising and Threat Calls of other individuals. Occasionally heard during daylight but usually at night. (5) **Bray**: agonistic Bray has faster delivery and higher pitch than sexual Bray. **Low Bray**: low-pitched exhaled component of Growl followed by brief inhaled trill. **Medium and Full Bray**: similar to Low Bray but more defined inhaled component and more highly pitched exhaled component; repeated 3–10 times/call. (6) **Hiss**: brief quiet exhalation covering wide range of frequencies. (7) **Aggressive Bark**: brief loud call covering wide band of frequencies. (8) **Aggressive Yell**: similar to Aggressive Bark, but of longer duration. (9) **Alarm Call**. When startled, penguins may squeak, but have no Alarm Call carrying obvious social information. (10) **Distress Call**. Occasionally make soft short repeated moan when confined in weighing bags, perhaps caused by distress. (11) **Contact Call**: short monosyllabic exhalant calls, described accurately as *huk*, *kuk* (Warham 1958) or *uk* (Hodgson 1975) and resembling yap of small dog. Birds making this call easily lured by crude imitations (Warham 1958). Made by penguins at sea and on



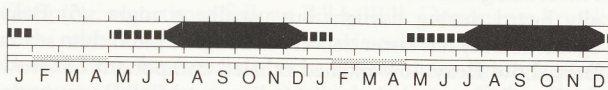
A J. Kendrick; P100

landing; most frequently about 1–2 h before sunrise when returning to sea (Montague 1982). **NON-VOCALSOUNDS.** Clicking sound made, probably by male, just before mounting during copulation (Hodgson 1975; Montague 1982; Warham 1958); not known whether this is a vocalization or non-vocal sound. Drumming sound made by male beating flippers on female's back during copulation, and when birds beat opponents with flippers during aggressive encounters and when being handled. Adults sneeze (Warham 1958).

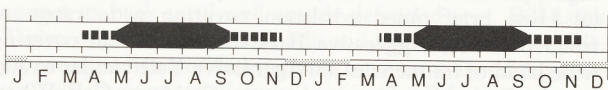
YOUNG (1) **Feeding Calls.** Young chicks (less than two weeks old) make soft sound when begging, probably adequately described as *peep, peep, peep*. Older chicks have louder persistent chirruping that resembles *pisst-pisst-pisst-pisst*. (2) **Alarm Call.** Chicks older than 2 weeks often hiss when lunging at intruder with their bills. Chicks sneeze (Warham 1958). Chicks before fledging heard making incomplete and varying Advertising Calls (P. Dann). No post-fledging calls recorded and no details on development of adult calls.

BREEDING Well known. Detailed studies in Aust. on Phillip I., Vic. (Reilly & Cullen 1979, 1981) and on Bruny I., Tas. (Hodgson 1975); in NZ at Wellington Harbour (Kinsky 1960) and at Otago (Gales 1984). Information supplied by P. Dann. Breed in simple pairs, usually loosely colonially, rarely solitarily; on islands and coastal areas; sometimes fortuitously associated with other seabirds such as shearwaters.

SEASON Broadly, Aug.–Feb. on Phillip I.; Apr.–Dec. on Penguin I., WA (Dunlop *et al.* 1988). On Phillip I., after moult between Feb. and Apr., birds continue to visit colony till laying starts; attendance increases from c. 20% in Week 16 to 70+% in Week 1 before laying, apparently with regular peaks at Weeks 7, 4 and 1 before laying; males generally present more often than females. Over 11 years, clutches started: May, 2; June, 2; July, 17; Aug., 58; Sept., 79; Oct., 73; Nov., 32; Dec., 11; mean dates of laying varied from 31 Aug. to 3 Nov. Approximate date of first eggs and duration of laying: Bruny I., 16 Sept.–8 Oct. in three seasons (8–11 weeks); Phillip I., (two exceptionally early layings in May) 29 June–29 Sept. in ten seasons (13–22 weeks); WA, Apr.; 26 weeks (Dunlop *et al.* 1988); Wellington, 1–20 Aug. in two seasons (14 weeks); Otago, 1 July and 16 Aug.–10 Dec. in two seasons (17 weeks); distinct drop in attendance at colony in Mar., Apr., May, between end of moult and start of breeding season. On Bruny and Penguin Is (Dunlop *et al.* 1988) birds apparently abandon colony after breeding.



a) Phillip I., se. Australia



b) Penguin I., sw. Australia

SITE Colonies mostly near sea in dune systems, grasslands and herbfields with good depth of soil for burrowing; also in crevices in talus below cliffs, and in caves, crevices along rocky coasts. Vegetation in nesting areas includes *Astelia*, *Phoenix* (Cunningham & Moors 1985), *Pterid-*

ium, *Cytisus*, *Phormium*, *Poa*, *Juncus*, *Scirpus*, *Disphyma* (Meredith 1984), *Tetragonia*, *Calocephalus*, *Rhagodia* and *Lomandra*. Nest up to 200 m inland (McManus 1979) and 50 m asl (White 1981) on accessible coastal slopes; up to 300 m inland on Gabo and Phillip Is. Burrowing and trampling by birds may create disturbance that allows invasion by introduced weeds at expense of native vegetation but no known association with particular plant communities. Good growth of vegetation probably helps to create protection from extremes of weather; in general, sites well sheltered and hidden. On Phillip I., 74% of burrows (n=434) on flat ground or on slopes of <10°. Thus, on cliffs or steep rises, burrows tend to be concentrated at bases and on shoulders. On undulating dune-systems distribution more even, probably because burrowing not restricted by depth of soil. On rocky areas, sites may be under rocks, in crevices and caves, under dense vegetation (tussock-grass *Poa* spp). In developed areas recorded nesting under houses, in outside lavatories, in culverts and drains, in overturned watering can, incinerators, breakwaters, among fuel drums; will accept artificial burrows (Reilly & Balmford 1975). Distance between burrows varies, usually not less than 2 m (Stahel & Gales 1987); but nests commonly <2 m apart in cave colonies (Waas 1990). Male may select site and probably takes greater share of digging and cleaning burrow but both sexes dig, using bill and feet; in NZ, male and female appear to select nest-site together (J.R. Waas). On Phillip I., birds tended to return to same part of colony year after year; half the pairs that stayed together used the same burrow; with a new mate, change of burrow more likely but males more likely than females to stay in same burrow; of 103 pairs that laid two or more clutches in a season, 29% changed burrows and were more likely to change after unsuccessful clutches. Shearwaters, rabbits, copperhead snakes and blue-tongued lizards may be found in burrows but not usually if Penguin there. Birds have twice been recorded incubating egg of Short-tailed Shearwater and once a litter of rabbits (P. Dann).

NEST, MATERIALS On Phillip I., lengths of burrows: 43 cm (17; 15–100; 100); entrances: 14 cm (5; 7–40; 100) high x 22 cm (7; 10–48) (P. Dann). Nests vary from a thick mat of grass and other plant material, rarely with some feathers, collected as available within 3–4 m (max. 6) of site, to only a few strands of vegetation (R. Gales). Both sexes gather material during night, males probably more than females, carrying it in beak and depositing directly into nest or gathering it at entrance and pulling it in later. Nests may be rebuilt in same burrow but material not known to be transferred from one burrow to another. Often dig more than one burrow before final selection. Excavation of burrows can be slow and take several weeks (R. Gales).

EGGS Ovoid or ovate; smooth textured; white, soon becoming stained, with sparse pin-head reddish dots noticeable when newly laid.

MEASUREMENTS:

Phillip I.: 54.6 (49.5–61.5; 60) x 42.0 (38.6–44.3) (P. Dann); Wellington: 56.4 (52.4–61.2; 41) x 43.1 (40.0–45.1); Mangere I., Chatham Is: 53.5 (1.82; 51.8–55.9; 4) x 40.7 (0.88; 39.6–41.6) (A.J.D. Tennyson). Otago: 56.1 (1.64; 53.2–59.6; 24) x 42.3 (1.03; 40.0–44.5); second-laid egg significantly shorter than first, but not less in volume.

WEIGHTS: Phillip I.: 53 (40–60; 60) (P. Dann);

Otago: 53.6 (3.61; 7) or 4.2% of adult weight.

CLUTCH-SIZE Bruny I., 92% of all clutches, C/2;

exceptions attributed to special circumstances. On Phillip I., 25 x C/1, 351 x C/2, 2 x C/3; in C/1s an egg could have been lost before or between inspections and in C/3s a second female could have been concerned (Reilly & Balmford 1975; Reilly & Cullen 1981). At Wellington, 70–75% of clutches, C/2.

LAYING Average interval 67.8 h (46–89; 24) (A. Hodgson); at Otago, all clutches laid in 3–5 days. Not synchronized (see above under Season). Second broods and replacement laying undertaken. At Bruny I., av. number of clutches per pair per year during four seasons, 1.05. At Phillip I., 1.38. At Wellington during two seasons, no second clutches after success and only 10% of failed pairs relaid. At Otago, second clutches recorded (Gales 1984). Interval between success and start of next clutch, 3–5 weeks at Phillip I.; at Otago, 11 days (9.29; 1–19; 3); between loss and replacement, 2–4 weeks (Reilly & Balmford 1972); 26 days (18–48; 18) at Bruny I.; 28 days (17.91; 9–52; 4) at Otago.

INCUBATION By both sexes. Because hatching of eggs occurs on same day (sometimes 2–4 days apart), probably full incubation usually starts before or at laying of second egg (Kinsky 1960; Gales 1984). Relief usually takes place in early hours of night (Gales 1984). Much variation of stints between individuals, throughout incubation period and perhaps from year to year. Kinsky found that birds (male or female) incubated for 16–17 h and were relieved for 6–7 h at night. Such short stints not recorded at Bruny and Phillip Is, where stints ranged from 1 to 8 days; some pairs alternated regularly every day. Kinsky recorded one observation of male, after returning from sea, feeding incubating female on nest. **INCUBATION PERIOD:** at Bruny I., 33.4 days (1.04; 50); at Phillip I., 33–37 days (Reilly & Balmford 1975); at Wellington, 33–43+ days (n=10) (all with marked eggs); on SI, NZ, 39 days (O'Brien 1940; marking of eggs not specified); at Otago, 36 days (2.5; 33–39; 8). Addled eggs incubated for 49, 49+, 70 days (Kinsky 1960). Birds accept eggs other than their own and may incubate stones, golf balls, tea-cups, etc. (Dann 1988). Eggshells trampled in nest but Kinsky noted removal to sea.

YOUNG Semi-altricial, nidicolous. Hatched with proptile slate-grey above, pale grey below; replaced by mesoptile after 8–14 days, dark grey to dark chocolate above, creamy white below; lores and area round eye bare till third week, then down-covered. Pin-feathers erupt at 4 weeks and down shed from underside of flippers and body. Last down retained as ruff round neck. By 8 weeks only sparse wisps remain, generally at junction of underside of flippers and body. Eye slits just open at one day, fully open at one week; iris changes from grey to pale grey at 5 weeks (Reilly & Balmford 1975). **NESTLING PERIOD:** at Bruny I., 54–63 days, once 78 days (n=11); at Phillip I., av. 58 days (n=76; Reilly & Balmford 1975); at Wellington, 49–63+ days (n=9); at Otago, 54 days (48–59; 18) (R. Gales). Attended by both parents. Brooded for first 10 days; then guard-stage (10–21 days) (or mean of 24 days at Otago) when one or another parent continuously with chicks, changing regularly each evening; next (21–28 days) intermediate stage during which one or other parent in attendance during night but leaving before daybreak, both parents returning regularly every night and feeding chicks; finally post-guard stage during which chicks are left alone except when parents come separately to feed them and leave soon afterwards; usually fed every night but in some years frequency of feeds may decline and young lose weight. Small crèches of 3–6 birds common in cave colonies (Waas 1990) but not elsewhere. Fed by incomplete regurgitation; until 3 weeks

old chicks put their heads inside parent's gape; later, adults insert mandibles inside those of chicks (Kinsky 1960). Defecation by chicks towards entrance of burrow or corners of nest-chamber.

GROWTH Weight at hatching: Phillip I., 36.7 g (4.8; 26–45; 50) (P. Dann); Otago: 45 g (1.15; 44–47; 3) (R. Gales) or 4% of average adult weight. Maximum rate of increase in weight at 20 days old; at fledging, mean weight 1148 g or 91% of adult weight (Stahel & Gales 1987). Maximum weight may be reached before fledging; apparently no decrease in weight in last days of nestling period (R. Gales).

FLEDGING TO MATURITY Young leave at night together or separately over 2–3 days; then independent of parents. At Phillip I., half the population breeds when 2 years old, other half when 3 years old (Dann & Cullen 1990).

SUCCESS Bruny I. over four seasons: hatching 68%, fledging 23%, total 16% and 0.32 chicks reared per pair. On Phillip I. over 11 seasons: hatching 65%, fledging 40%, total 26% and 0.71 chicks reared per pair. At Wellington over two seasons: hatching 54%, 59%, fledging 86%, 94%, total 50%, 51%. At Otago in one season, hatching 63%, fledging 75%, total 47%; 1.6 chicks per successful pair and 0.95 chicks for all pairs (Gales 1984). Mean annual survival of breeding adults on Phillip I. 85.8%, giving life expectancy of 6.5 years. At Bruny I., mean annual survival, 57.2%. At Otago, chief cause of egg-loss, heavy rain. In e. Tas. chief predators are fishermen killing birds for bait (HASB). On Phillip I., foxes and dogs chief predators (P. Dann). Pacific Gulls *Larus pacificus* take chicks and even adults; Tiger Snakes *Notechis ater* take chicks and eggs (HASB). New Zealand Fur Seals take adults in NZ and Aust. (Notman 1985; S. Goldsworthy); Australian Fur Seals have not been recorded taking Penguins (Warneke & Shaughnessy 1985). Birds killed during storms (HASB). On Bruny and Phillip Is endangered by human activities: road kills, trampling, housing development, erosion, weeds, introduced predators and some land use (A. Hodgson; P. Dann). On De Witt I., three fires in 1975 and 1976 killed 1000 breeding adults and many chicks (White 1979). Internal parasites increase effects of exhaustion and food shortage (Obendorf & McColl 1980; C. Harrigan).

PLUMAGES

Subspecies *novaehollandiae*.

ADULT HEAD AND NECK. In fresh plumage: frons, crown and lores, pale dark-brown (121); feathers fringed dark blue-grey (78). Feathers below eye and on cheeks, light grey (85); dark grey (84) near ear; few feathers fringed light blue-grey (88). Chin to lower neck, white; concealed base of feathers, very pale dark-brown (121); whiteness manifest as broad fringe; rachis from throat to lower neck, brown (119B). Feathers of nape and hindneck, short, dense, similar to crown. In worn plumage, before moult, base of feathers on side of neck and face, very pale dark-brown (121); paler at chin and throat; base of feathers exposed. **UPPERPARTS.** Mantle, back and rump, short, dense, similar to crown. Upper tail-coverts similar, but fringed light blue-grey (88). All rachis on dorsum, laterally flattened and black (89). **TAIL,** white. **UPPERFLIPPER,** similar in colour to back; feathers, scale-like anteriorly, longer posteriorly, ordered in distinct rows; two posterior rows, white. In worn plumage, black (89). **UNDERPARTS.** Upper breast to under tail-coverts, including inner thighs, white; slight inward progression of white feathers extending towards back, near axilla and extending as straight line to thighs. Outer margin of flanks and hind thighs, similar to back, but fringed

light blue-grey (88). Scattered white filoplumes near base of axilla. Rachis, white from upper breast to vent. UNDERFLIPPER, white with small black (89) patch near distal tip. For full description of plumage changes during moult see Richdale (1940) and Kinsky (1960).

DOWNY YOUNG Protoptile down short but dense. Down near lores, ears to nape, forms dark-brown (219) cap. Lores and round eye bare (Reilly & Balmford 1975). Chin to lower throat, sides of neck and upperparts, pale dark-brown (219). Small white patch of down on midline of upper neck. Down from upper breast to vent, light grey-brown (119D). Dorsal surface of flipper, similar to upperparts. Posterior margin and underside of flipper, light grey-brown (119D). Mesoptile thicker on crown and hindneck, short but dense; longer on rump. Down on crown and dorsum, dark brown (119A), slightly darker at lores. Chin to throat, white with light grey-brown (119D) tips. On thighs, flanks and lower neck, down paler (c119C). Upper breast to vent, down thicker, woolly and white. Flipper, dorsal surface dark brown (119A); distal margin, light grey-brown (c119D). Ventral surface of flipper, white. See Richdale (1940), O'Brien (1940), Reilly & Balmford (1975) and Gales (1984) for details of plumage development to juvenile.

JUVENILE Similar to adult except fringes of feathers on dorsum, light blue-grey (88); grey (84) round ear, lighter grey (85) under eye.

Subspecies *albosignata*.

ADULT Has more distinctive plumage than other subspecies; largest *Eudyptula* in NZ. **HEAD AND NECK.** Auricular area and cheeks, light grey. **UPPERPARTS.** Dorsum, light Columbia-blue (Ridgway 1912, pl. XXXIV). Lower rump, sometimes white. **TAIL,** white with black rachis, blue with black rachis, or bicoloured. **UPPERFLIPPER** has triple row of white feathers on posterior margin. At carpal flexure, broad white patch (mostly in males), which in some birds may fuse with white anterior margin. Anteriorly, broad white band. **UNDERFLIPPER,** white with small black patch at tip.

DOWNY YOUNG Differs from all other NZ subspecies in having white down on ventral surface of flipper, continuing onto posterior margin (O'Brien 1940); requires further study.

Nominate *minor*.

ADULT HEAD AND NECK. Auricular area and cheeks, dark slaty-grey. **UPPERPARTS.** Dorsum, indigo-blue (Ridgway 1912, pl. XXXIV). **TAIL,** similar to dorsum. **UPPERFLIPPER;** double row of white feathers on posterior margin. Anteriorly, similar to dorsum. **UNDERFLIPPER,** white with black patch of varying size at tip.

Subspecies *chathamensis*.

Similar to *E.m. minor*, though dorsum slightly lighter. Differs principally in measurements and colour of iris (see appropriate sections).

Subspecies *variabilis*.

ADULT HEAD AND NECK. Auricular area and cheeks, brownish grey. **UPPERPARTS.** Dorsum, Tyrian-blue (Ridgway 1912, pl. XXXIV); colour varies, similar to *E.m. minor* and *E.m. iredalei* at extremes. **TAIL,** similar to *E.m. minor*, but some birds have white patch on upper tail-coverts. **UPPERFLIPPER;** usually two, but sometimes three, posterior rows of white feathers. Anteriorly, sometimes has white margin. **UNDERFLIPPER.** Similar to *E.m. minor*.

Subspecies *iredalei*.

UPPERPARTS, light Tyrian-blue (Ridgway 1912, pl. XXXIV). Otherwise similar to *E.m. variabilis*. Some adults

and juveniles have white anterior margin to flipper (Jones 1978; see Aberrant plumages).

ABERRANT PLUMAGES Albinism and partial albinistic birds recorded in all subspecies (Jones 1978; C. Challes). In *E.m. iredalei*, white band 3–6 mm wide observed on anterior margin of flipper in about 2% of population in both adults and juveniles. Dark V-marking noted in cloacal area; marking, prominent or reduced (Jones 1978).

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

ADULT Iris, brownish grey (79) with dull white inner ring adjoining pupil. Bill, grey-black (82); base of lower mandible, pink-buff (121D). Legs and feet, white with strong pink (7) shade. Claws, soles and tips of webs, dull black (89).

DOWNY YOUNG Iris dark grey, changing to pale grey at c. 5 weeks, with dark outer rim resembling that of adult. At hatching, bill black at end of first week; basal two-thirds of lower mandible pale grey, similar to adult's. Small white egg-tooth; remains for 6 weeks, with small remaining mark noticeable throughout pre-fledging period (Reilly & Balmford 1975). In nominate *minor*, egg-tooth present for 22–28 days (Gales 1984). Feet change from pale grey at hatching to off-white at 3 weeks. Claws, webs and soles change from dark grey to black at 3 weeks (Reilly & Balmford 1975).

JUVENILE Similar to adult, except two-thirds of base of lower mandible and base of upper, pale grey (86) to grey-mauve (77). Black (89) on webs more extensive.

In NZ subspecies:

ADULT Iris, similar to *novaeollandiae*, except in *chathamensis*, which has bluish grey, sometimes hazel, iris (Kinsky & Falla 1976). Full details of iris colour in *albosignata* in O'Brien (1940). Colour of bill, legs and feet similar to *novaeollandiae*.

DOWNY YOUNG Description of bare parts of *albosignata* in O'Brien (1940); *variabilis* in Kinsky (1960); *minor* in Gales (1984).

JUVENILE Similar to *E.m. novaeollandiae*.

MOULTS

ADULT POST-BREEDING Differs between breeders and non-breeders and between successful and unsuccessful breeders (Reilly & Cullen 1983; Gales 1984). Complete; usually occurs on breeding grounds, in burrow. Molt either simultaneous among pairs, or with some asynchrony of start. *E.m. novaeollandiae*: earliest initiation of moult at Phillip I., Vic., in 13 years (Reilly & Cullen 1983), 31 Jan.; latest, 8 June; 75% of birds moulted between 8 Feb.–23 Mar. No annual difference in timing of moult recorded from 1969–71. Duration of moult, 17.7 days (15–20). In Tas., timing of moult similar; though 9 days earlier, with mid-moult date, 20 Feb. Hodgson (1975) gives starting dates for 4 years; other notes in Reilly and Cullen (1983). Warham (1958) gives starting date in Bass Str. as 18 Jan.; duration as 17–18 days. At Penguin I., WA, moult earliest in Aust., Dec.–Feb. (Klomp & Wooller 1988a,b). Captive birds started moult early, Dec.–Mar.; duration, c. 2 weeks (Baudinette *et al.* 1986). First signs of moult; rectrices replaced and colour of mouth and throat becomes pale, presumably anaemic (Baudinette *et al.* 1986).

In NZ subspecies, moult earlier than in se. Aust.; *iredalei*: moult-period, late Dec.–Mar.; most in Feb. (Jones 1978); *variabilis*: moult-period, Dec.–Mar.; in 1956–57, average moult date 24 Jan.; duration 15.5 days (12–18) (Kinsky 1959, 1960);

albosignata: moult starts 9 Jan.; duration 10–14 days (O'Brien 1940). Nominat *minor*: at Taiaroa Head, SI, NZ, in 1983 (Gales 1984), moult started 21 Jan.; last moult 3 Apr. Moult simultaneous among pairs, though some asynchrony recorded. Eleven non-breeding adults moulted significantly earlier than twelve breeding adults; mean date 5 Feb.; duration 16.4 days (10.45; 11). Successful breeders moulted for 33.0 days (17.90; 8) ($P < 0.05$). No difference in timing between non-breeders and unsuccessful breeders. Duration of moult in colony, 16.2 days (0.98; 15–18; 11). Comparison between successful and failed breeders in Gales (1984). Moult undescribed in other subspecies.

POST-JUVENILE Complete; as for non-breeders.

MEASUREMENTS BILL D (G) = bill depth at gonys; BILL D (B) = bill depth at base of culmen; TARSUS(F) = tarsus measured from front; TARSUS(D) = tarsus measured diagonally.

Nominat *minor*. (1) Southland, Stewart I. and Westland, adults, skins; methods described (Kinsky & Falla 1976). (2) Otago Coast, adults, skins; methods described; bill measurements for females obviously in error (Kinsky & Falla 1976).

| | MALES | FEMALES |
|------------|--|---|
| FLIPPER | (1) 118.1 (4.41; 112–126; 7) (2) 124.2 (3.25; 120–129; 11) | 117.0 (3.91; 111–124; 7) 119.4 (5.0; 111–129; 9) |
| BILL | (1) 35.7 (2.24; 31.4–40.1; 14) (2) 38.9 (2.51; 34.6–43.2; 11) | 34.5 (1.59; 31.8–36.8; 13) 32.2 (1.32; 35–38.6; 9) |
| BILL D (G) | (1) 15.4 (1.46; 13–18.6; 14) (2) 15.2 (1.13; 13.6–17.4; 11) | 14.1 (1.41; 11.6–17.2; 13) 13.3 (0.89; 12.3–14.7; 9) |
| TARSUS | (1) 18.4 (2.14; 16.2–22.6; 7) (2) 18.5 (1.47; 15.7–20.8; 11) | 19.0 (0.79; 17.8–20.2; 7) 18.3 (1.87; 15.6–21.8; 9) |
| TOE | (1) 54.5 (1.44; 52.1–56.1; 7) (2) 55.2 (2.41; 52.1–58.6; 11) | 51.2 (2.47; 47.2–54.5; 7) 52.6 (3.63; 44.3–55.8; 9) |

Subspecies *albosignata*. (3) Central Canterbury coast, Otago, Cook Str., skins; methods described (Kinsky & Falla 1976).

| | MALES | FEMALES |
|------------|--------------------------------|----------------------------|
| FLIPPER | (3) 126.0 (3.24; 120–130; 12) | 124.6 (2.83; 114–129; 11) |
| BILL | (3) 39.0 (2.03; 36.8–43.6; 26) | 36.3 (1.93; 32.4–41.0; 21) |
| BILL D (G) | (3) 17.0 (1.44; 14.6–19.8; 25) | 15.4 (1.51; 11.8–17.3; 21) |
| TARSUS | (3) 21.0 (1.93; 18.2–24.5; 13) | 19.5 (1.23; 17.1–21.5; 11) |
| TOE | (3) 54.5 (2.48; 49–58.2; 13) | 53.9 (1.75; 50.8–56.2; 11) |

Subspecies *chathamensis*. (4) Chatham Is, adults, skins; methods described (Kinsky & Falla 1976).

| | MALES | FEMALES |
|------------|--------------------------------|----------------------------|
| FLIPPER | (4) 124.2 (2.6; 120–129; 12) | 120.4 (4.39; 113–129; 13) |
| BILL | (4) 38.1 (2.26; 34.2–40.2; 20) | 34.8 (1.43; 32.5–36.7; 13) |
| BILL D (G) | (4) 18.3 (0.65; 17.2–19.6; 19) | 16.3 (0.54; 14.4–17.1; 13) |
| TARSUS | (4) 21.2 (2.86; 17.5–24.3; 12) | 21.3 (2.70; 17.2–24.1; 7) |
| TOE | (4) 56.2 (1.44; 51.8–61.1; 13) | 54.9 (2.47; 53.6–56.5; 7) |

Subspecies *variabilis*. (5) Coasts and islands of s. NI and n. SI, adults, skins; methods described (Kinsky & Falla 1976).

| | MALES | FEMALES |
|------------|--------------------------------|----------------------------|
| FLIPPER | (5) 124.5 (4.53; 114–138; 30) | 120.5 (3.92; 109–129; 21) |
| BILL | (5) 37.4 (1.43; 33.5–40.9; 74) | 35.9 (1.37; 31–37.8; 71) |
| BILL D (G) | (5) 16.0 (0.82; 13.9–18.8; 75) | 13.6 (0.72; 11.2–16.4; 69) |
| TARSUS | (5) 20.9 (2.87; 17.5–26.6; 40) | 20.7 (2.28; 16.1–26.8; 22) |
| TOE | (5) 54.2 (2.95; 46.1–59.1; 30) | 51.5 (2.67; 47.1–57.7; 22) |

Subspecies *iredalei*. (6) Coasts and islands of n. NI, adults, skins; methods described (Kinsky & Falla 1976).

| | MALES | FEMALES |
|------------|--------------------------------|----------------------------|
| FLIPPER | (6) 116.3 (3.62; 108–121; 33) | 114.3 (3.77; 109–121; 17) |
| BILL | (6) 35.8 (1.56; 31.8–40.4; 43) | 33.8 (1.84; 29.8–40.4; 29) |
| BILL D (G) | (6) 14.2 (1.13; 11.6–16.4; 43) | 12.8 (0.71; 11.4–14.6; 28) |
| TARSUS | (6) 18.6 (1.63; 15.6–24.3; 33) | 17.6 (2.34; 14–22.8; 29) |
| TOE | (6) 49.6 (2.47; 45.5–56.2; 33) | 47.6 (3.41; 41.2–53.5; 14) |

Subspecies *iredalei*. (7) Tiritiri Matangi I., adults, live; methods described (Jones 1978).

| | MALES | FEMALES |
|------------|---------------------------|--------------------------|
| FLIPPER | (7) 110.3 (5.6; 98–120) | 105.0 (5.7; 89–112) ** |
| BILL | (7) 36.2 (2.2; 29.1–37.7) | 34.0 (1.8; 32.4–41.2) ** |
| BILL D (G) | (7) 14.2 (0.9; 11.9–15.3) | 12.3 (0.5; 11.3–13.4) ** |
| BILL D (B) | (7) 16.2 (1.1; 14.8–19.9) | 14.2 (0.8; 12.7–15.5) ** |

Subspecies *E.m. novaehollandiae*. (8) NSW, Vic., Tas., SA, WA, adults, skins; methods described (Kinsky & Falla 1976). (9) S. Tas., freshly dead; sexed by dissection; methods described (Phillips 1960). (10) S. Tas., mated pairs during breeding season, live; sexed by cloaca; methods described (Phillips 1960). (11) Phillip I.; sexed by dissection (P. Dann).

| | MALES | FEMALES |
|------------|---|--|
| FLIPPER | (9) 120.4 (2.25; 117–125; 12) (10) 120.6 (2.49; 116.5–124; 22) | 117.3 (2.54; 112–120; 8) 117.6 (3.52; 112–124; 22) |
| TAIL | (9) 29.2 (1.48; 27–32; 7) | 28.6 (1.49; 26–30; 5) |
| BILL | (8) 37.7 (2.18; 31.3–41.7; 26) (9) 39.4 (1.49; 37–42; 12) (10) 38.8 (1.61; 36.3–42.5; 22) (11) 39.2 (2.55; 68) | 36.5 (2.23; 32.5–39.8; 20) 37.7 (1.85; 35–40; 8) 36.5 (1.05; 34.5–39.6; 22) 36.5 (1.85; 86) |
| BILL D (G) | (8) 14.0 (1.01; 11.9–16.2; 23) (9) 15.5 (0.75; 15–17; 12) (10) 14.3 (0.67; 13.1–15.4; 22) | 13.4 (1.22; 11–16.8; 18) 13.7 (0.69; 13–15; 7) 12.2 (0.48; 11.4–13.1; 22) |
| BILL W (B) | (9) 13.1 (1.06; 11–15; 12) | 12.2 (0.96; 11–14; 8) |
| TARSUS(F) | (9) 28.8 (0.93; 27–30; 11) | 29.1 (1.45; 27–32; 8) |
| TARSUS(D) | (9) 34.8 (1.33; 33–38; 11) | 34.2 (1.56; 32–37; 8) |
| TOE | (9) 50.7 (1.92; 48–54; 12) (10) 49.0 (1.37; 46–52; 22) | 48.1 (1.69; 45–50; 8) 47.2 (1.85; 43–50; 22) |

Statistical comparisons of measurements of *iredalei* with other subspecies in Jones (1978). Growth rates of chicks in Richdale (1940), Hodgson (1975), Jones (1978) and Gales (1984, 1987).

WEIGHTS Nominat *minor*. (1) Southland, Stewart I. and Westland, adults, skins, dates unknown (Kinsky & Falla 1976). (2) Otago coast, adults, skins, dates unknown (Kinsky & Falla 1976).

| | MALES | FEMALES |
|-----|--------------------------------|------------------------------|
| (1) | 1063 (187.4; 911-1360; 5) | 945 (112.3; 800-1097; 5) |
| (2) | 1243.7 (127.25; 1080-1475; 10) | 1085.2 (148.68; 895-1374; 9) |

Subspecies *albosignata*. (3) Central Canterbury coast, Otago, Cook Str., skins, dates unknown (Kinsky & Falla 1976).

| | MALES | FEMALES |
|-----|-------------------------------|------------------------------|
| (3) | 1357.5 (182.5; 1067-1546; 11) | 1279.7 (164.8; 1108-1500; 7) |

Subspecies *chathamensis*. (4) Chatham Is, adults, skins, dates unknown (Kinsky & Falla 1976).

| | MALES | FEMALES |
|-----|--------------------------|---------------------------|
| (4) | 1190 (122; 991-1412; 13) | 1017 (146.9; 793-1203; 6) |

Subspecies *variabilis*. (5) Coasts and islands of s. NI and n. SI, adults, skins, dates unknown (Kinsky & Falla 1976).

| | MALES | FEMALES |
|-----|------------------------------|------------------------------|
| (5) | 1167.7 (109.2; 950-1420; 28) | 1045.3 (121.6; 820-1238; 20) |

Subspecies *iredalei*. (6) Coasts and islands of n. NI, adults, skins, dates unknown (Kinsky & Falla 1976).

| | MALES | FEMALES |
|-----|-----------------------------|---------------------------|
| (6) | 934.6 (96.59; 752-1055; 11) | 841.5 (110.7; 698-956; 6) |

Subspecies *novaehollandiae*. (7) Vic., mostly Phillip I. (P. Dann).

| | MALES | FEMALES |
|-----|------------------------------|------------------------------|
| (7) | 1172 (164; 550-2130; 12 278) | 1048 (159; 550-2100; 10 973) |

Weight varies with season, sex and age. Peak weights occur during onset of moult; lowest during moult. Males generally heavier than females; adults heavier than juveniles. Weight loss in *novaehollandiae* during moult summarised in Hodgson (1975). Gales (1984) gives weight at start of moult of breeding *minor* at Taiaroa Head, SI, as 1922 (96.7; 10); no significant difference from that of non-breeders 1916 (212.2; 10). Mean weight loss during moult, 882 g (54 g/day), representing loss of 46% of initial weight. Weight loss linear with time (Gales 1984). Weight loss during moult in *variabilis* estimated at 40-50% (Kinsky 1960); in *iredalei*, 30-40% (Jones 1978). Examples of seasonal variation in weights of *variabilis* in Kinsky (1960); *novaehollandiae* (Hodgson 1975); *iredalei* (Jones 1978); *minor* (Gales 1984). Summary of mean body weights for all subspecies, most in non-moulting season, in Klomp & Wooller (1988a,b); these weights more accurately reflect subspecific differences than other measurements currently available; w. Aust. populations are heaviest of all sub-

species. General summary of weight loss for moulting birds in Croxall (1982). Details of weight changes in chicks in Richdale (1940), Kinsky (1960), Hodgson (1975), Jones (1978), Montague (1982) and Gales (1984, 1987).

STRUCTURE Flightless. Smallest penguin. Flipper, hard and bony, short and narrow. Feathering of body dense, strongly lanceolate; rachis broad and flattened at tips; imparts glossy appearance. About 14 rectrices, t1 longest. Ventral surface of rachis on rectrices concave. Tail, short and wedge-shaped; in *novaehollandiae*, calamus and rachis transparent near base. Bill slender; culminicorn rounded; hooked at tip; bill profiles for all subspecies in Kinsky & Falla (1976). Legs very short. Pads of soles thick. Claws, long and curved. Outer toe c. 89% of middle, inner c. 62%; hind, small, c. 12%. Two preen-glands noticeable in protoptile down; not noticeable in juvenile plumage (Reilly & Balmford 1975).

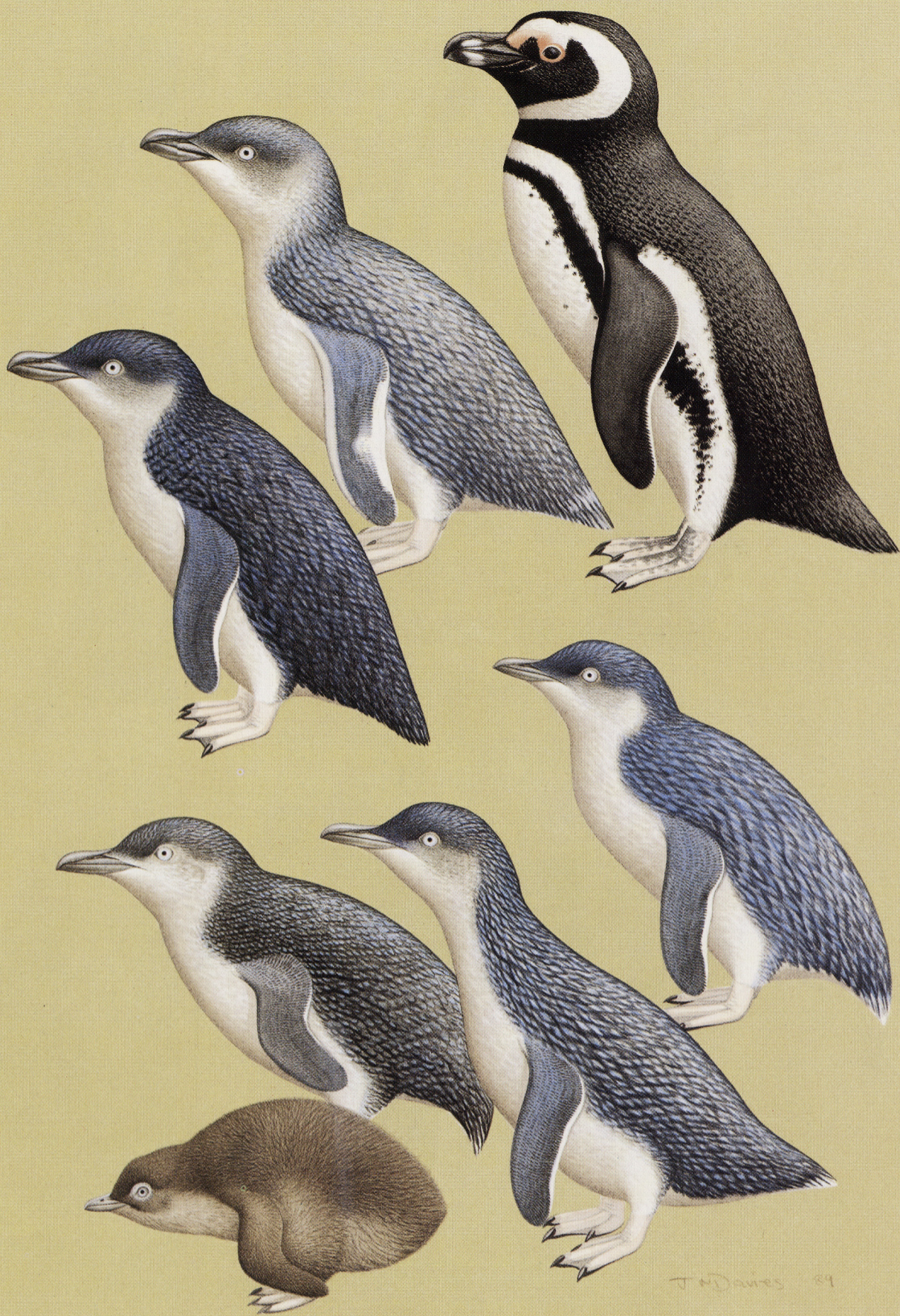
SEXING, AGEING Adults on bill measurement (sexually dimorphic); in all subspecies, depth and length of bill greater in males than in females. Details in Richdale (1940), O'Brien (1940), Kinsky (1960), Phillips (1960), Reilly & Balmford (1975), Kinsky & Falla (1976), Jones (1978), Meredith (1984) and Gales (1984, 1988). Jones (1978) sexes *iredalei* using depth-index criterion. Gales (1988) gives discriminant function analysis and sex-classification criteria for *novaehollandiae*; unreliable for use with other subspecies because of variation in bill dimensions. Key for ageing chicks using plumage and structural criteria (sexable for up to c. 4 weeks) in Gales (1984) and Stahel and Gales (includes illustrations; 1987). Sexable on cloaca (Serventy 1956; Phillips 1960; Gales 1988).

GEOGRAPHICAL VARIATION Six subspecies recognized; major criteria for separation: dorsal colour, dimensions of bill, and weight; some minor criteria (Kinsky & Falla 1976). Ranges as follows: in NZ: *minor*, w. and s. coasts of SI, including Stewart I.; *albosignata*, Banks Pen. and Motunau I.; *chathamensis*, Chatham Is; *iredalei*, n. part of NI; *variabilis*, Cook Str. In Aust.: *novaehollandiae*, s. coast and outlying islands, including Tas. (details in NZCL; Kinsky & Falla 1976). Use of some diagnostic characters in subspecific identification, particularly dorsal colour and body weight, criticized by Jones (1978) and Meredith & Sin (1988a). No variation in Aust., though w. populations larger than any subspecies; presumably related to warm climate and food supply linked to Leeuwin Current (Klomp & Wooller 1988a,b). Clinal variation of size and colour from S to N recorded on e. coasts of NZ, between *albosignata*, *variabilis* and *iredalei*; clinal variation supported by genetic study (Meredith 1984; Meredith & Sin 1988a,b); but criticised on basis of discrete rather than broad sampling localities, and omission of nominate *minor* from study (J.R. Waas). Large size and white anterior flipper margins in some birds link populations of *minor* on Otago coast with *albosignata* (Kinsky & Falla 1976; C. Challies). Interbreeding between *albosignata* and *variabilis* may occur (Kinsky & Falla 1976; Meredith & Sin 1988a); needs further study. Further study of NZ populations needed to test validity of subspecies (Jones 1978; R. O'Brien).

REFERENCES

- Barton, D. 1978. *Corella* 2: 71-2.
 Barton, D. 1979. *Emu* 79: 141-2.
 Baudinette, R.V., & P. Gill. 1985. *J. Comp. Physiol.* 155: 373-80.

- Baudinette, R.V., et al. 1986. *Aust. J. Zool.* 34: 35-45.
- Bowker, G.M. 1980. *Corella* 4: 104-6.
- Brothers, N.P. 1983. *Corella* 7: 91-2.
- Burger, J. 1987. Unpubl. Senior thesis, Univ. California.
- Carter, T. 1910. *Emu* 10: 137.
- Clark, B.D., & W. Bemis. 1979. *J. Zool., Lond.* 188: 411-28.
- Costa, D.P., et al. 1986. *Comp. Biochem. Physiol.* 85A: 135-8.
- Croxall, J.P. 1982. *J. Anim. Ecol.* 51: 177-94.
- Cunningham, D.M., & P.J. Moors. 1985. *Notornis* 32: 221-43.
- Dann, P. 1988. *Emu* 88: 101-103.
- Dann, P. 1991. *Emu* 91 (Suppl.).
- Dann, P., & J.M. Cullen. 1989. *Corella* 13: 34-7.
- Dann, P., & J.M. Cullen. 1990. Pp 63-84. In: Davis & Darby 1990.
- Dann, P., et al. 1991. *Emu* 91.
- Davis, L.S. & J.T. Darby (Eds). 1990. *Penguin Biology*.
- Dove, H.S. 1910. *Emu* 9: 252-4.
- Dunlop, J.N., et al. 1988. *Corella* 12: 93-8.
- Eckert, J. 1971. *Emu* 71: 61-4.
- Gales, R. 1984. Unpubl. M.Sc. thesis, Univ. Otago.
- Gales, R. 1987. *Emu* 87: 212-19.
- Gales, R. 1988. *Notornis* 35: 71-5.
- Gibson, J.D. 1976. *Aust. Bird Bander* 14: 100-103.
- Gillham, M.E. 1961. *Proc. R. Soc. Vict.* 74: 21-35.
- Green, R.H. 1973. *Aust. Bird Bander* 11: 81-3.
- Guthrie-Smith, H. 1914. *Mutton Birds and Other Birds*.
- Harris, M.P., & F.I. Norman. 1981. *Mem. nat. Mus. Vic.* 42: 89-106.
- Harris, M.P., & K.G. Bode. 1981. *Emu* 81: 20-8.
- Harris, M.P., & D.M. Deerson. 1980. *Corella* 4: 69-70, 71-2, 73-4, 75-6, 79-80, 85-6, 87-8.
- Harris, M.P., et al. 1980. *Corella* 4: 93-5.
- Hodgson, A. 1975. Unpubl. Ph.D. thesis, Univ. Tasmania.
- Jones, G. 1978. Unpubl. MSc thesis, University of Auckland.
- Jouventin, P. 1982. *Visual and Vocal Signals in Penguins*.
- Kinsky, F.C. 1959. *Proc. NZ Ecol. Soc.* 6: 12-15.
- Kinsky, F.C. 1960. *Rec. Dom. Mus.* 3: 145-218.
- Kinsky, F.C., & R.A. Falla. 1976. *Rec. Nat. Mus. NZ* 1: 105-26.
- Klomp, N. 1987. *Bull. Ecol. Soc. Aust.* 17: 9-10.
- Klomp, N.I., & R.D. Wooller. 1988a. *Rec. West. Aust. Mus.* 14: 211-15.
- Klomp, N.I., & R.D. Wooller. 1988b. *Aust. J. mar. freshwat. Res.* 39: 633-9.
- Lashmar, A.F.C. 1987. *Corella* 11: 89-92.
- Lindsey, T. 1986. *The Seabirds of Australia*.
- Ling, J.K. & M.M. Bryden (Eds). 1985. *Studies of Sea Mammals in South Latitudes*.
- McManus, T.J. 1979. *Corella* 3: 52-4.
- Meredith, M.A.M. 1984. Unpubl. M.Sc. thesis, Univ. Canterbury.
- Meredith, M.A.M., & F.Y.T. Sin. 1988a. *J. Nat. Hist.* 22: 801-809.
- Meredith, M.A.M., & F.Y.T. Sin. 1988b. *Heredity* 60: 69-76.
- Mill, G.K., & J. Baldwin. 1983. *Physiol. Zool.* 56: 242-54.
- Milledge, D. 1977. *Corella* 1: 1-12.
- Montague, T.L. 1982. Unpubl. M.Sc. thesis, Monash Univ.
- Montague, T.L. 1985. *Emu* 85: 264-7.
- Montague, T.L., & J.M. Cullen. 1988. *Emu* 88: 138-49.
- Norman, F.I., et al. 1980. *Proc. R. Soc. Vic.* 91: 135-54.
- Norris, A.Y. 1965. *Notornis* 12: 80-2.
- Notman, P. 1985. *Notornis* 32: 260.
- Obendorf, D.L., & K. McColl. 1980. *J. Wildl. Diseases* 16: 251-9.
- O'Brien, P.J. 1940. *Rec. Cant. Mus.* 4: 311-24.
- Parker, S.A., et al. 1979. *An Annotated Checklist of the Birds of South Australia*.
- Pescott, T. 1965. *Vict. Nat.* 81: 290-301.
- Pescott, T. 1983. *Birds of Geelong*.
- Phillips, A. 1960. *Proc. R. Soc. Tas.* 94: 63-67.
- Phillips, A. 1961. *Pap. Proc. R. Soc. Tas.* 94: 63-72.
- Reilly, P.N. 1974. *Emu* 74: 198-200.
- Reilly, P.N. 1977. *Corella* 1: 51-3.
- Reilly, P.N. 1978. *A'sian Seabird Grp Newsl.* 10: 20-1.
- Reilly, P.N., & P. Balmford. 1972. *Aust. Bird Bander* 10: 8-10.
- Reilly, P.N., & P. Balmford. 1975. Pp 161-87. In Stonehouse 1975.
- Reilly, P.N., & J.M. Cullen. 1979. *Emu* 79: 97-102.
- Reilly, P.N., & J.M. Cullen. 1981. *Emu* 81: 1-19.
- Reilly, P.N., & J.M. Cullen. 1982. *Emu* 82: 137-42.
- Reilly, P.N., & J.M. Cullen. 1983. *Emu* 83: 94-8.
- Richdale, L.E. 1940. *Emu* 40: 180-217.
- Ridgway, R. 1912. *Colour Standards and Colour Nomenclature*.
- Roberts, T.M. 1951. *Notornis* 4: 164.
- Robertson, C.J.R., & B.D. Bell. 1984. *ICBP Tech. Publ.* 2: 573-86.
- Schulz, M. 1987. *Emu* 87: 186-187.
- Serventy, D.L. 1956. *Emu* 56: 213-14.
- Stahel, C., & R. Gales. 1987. *Little Penguin: Fairy Penguins in Australia*.
- Stonehouse, B. (Ed.). 1975. *The Biology of Penguins*.
- van Tets, G.F. 1977. *Corella* 1: 63-4.
- Waas, J.R. 1988a. Unpubl. Ph.D. thesis, Univ. Canterbury.
- Waas, J.R. 1988b. *Animal Behaviour* 36: 366-71.
- Waas, J.R. 1990. In: Davis & Darby 1990.
- Waas, J.R. In press. *Behaviour*.
- Warham, J. 1958. *Ibis* 100: 605-616.
- Warham, J. 1979. *Corella* 3: 42-5.
- Warneke, R.M., & P.D. Shaughnessy. 1985. Pp 53-75. In: Ling & Bryden 1985.
- Weavers, B. 1987. Pp 26-31. *Little Penguin Research Programme: Interim Rep.* DCFL, Vict.
- White, G. 1979. *Corella* 3: 61-2, 63-5.
- White, G. 1981. *Corella* 5: 53-5.



J. Davies '89

Volume 1 (Part A), Plate 12

Little Penguin *Eudyptula minor*

1. Adult, subspecies *novaeollandiae*, fresh
2. Adult, subspecies *novaeollandiae*, worn
3. Juvenile, subspecies *novaeollandiae*
4. Adult, subspecies *minor*, fresh
5. Adult, subspecies *albognata*, fresh
6. Downy young, subspecies *novaeollandiae*

- Magellanic Penguin *Spheniscus magellanicus*
7. Adult male

© Jeff Davies

